THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

December 16, 1981 Paper 106

LARGER BIVALVE ARTHROPODS FROM THE MIDDLE CAMBRIAN OF UTAH[1]

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Abstract—Carapaces or valves of 12 species of larger bivalve arthropods and one species of an associated univalve arthropod are described from Middle Cambrian strata of northern and western Utah. Some of these bivalve species represent phyllocarid Malacostraca whereas others may represent either phyllocarids or Branchiopoda. Affinity of the univalve species is less certain. One genus and five species of larger bivalves are new, the new genus being *Dicerocaris* and the new species being *Dicerocaris opisthoeces, Perspicaris? dilatus, Perspicaris? ellipsopelta, Tuzoia guntheri,* and *Tuzoia? peterseni.* Specimens of *Branchiocaris?* sp., *Canadaspis* cf. *C. perfecta* (Walcott), *Dioxycaris argenta* (Walcott), *Proboscicaris agnosta* Rolfe, *Pseudoarctolepis sharpi* Brooks and Caster, *Tuzoia retifera* Walcott, and an undetermined genus and species are illustrated and discussed. Three distinctive univalve carapaces are assigned to the new genus and new species *Pahvantia hastata.* Collectively, the specimens provide important information concerning the distribution and species diversity of a poorly known element of the Cambrian fauna.

EXTENSIVE SEARCHES and generous contributions by several persons during the past two decades have made possible the assembly of a collection of more than 100 carapaces or disarticulated valves of larger bivalve arthropods from Middle Cambrian strata in Utah (Fig. 1). Because in life the exoskeletons of these arthropods were not mineralized, their preservation is uncommon. To our knowledge, the only larger collection of such Cambrian fossils is that from the famous Burgess Shale in British Columbia. This paper includes descriptions of 12 larger bivalve arthropod species and one probable univalve species.

Larger bivalve arthropods have been reported from few Cambrian formations in North America. Several species, some of which we consider to be synonyms, have been described from the Burgess Shale of Middle Cambrian age (Walcott, 1912a; Resser, 1929;

[1]Manuscript received August 21, 1981.

Rolfe, 1962; Simonetta and Delle Cave, 1975; Briggs, 1976, 1977, 1978). Distribution elsewhere in western North America, includes three species from the Eager Formation of Early Cambrian age in British Columbia (Resser, 1929); one species from the Ophir Shale (Walcott, 1886) and another from the Wheeler Formation (Brooks and Caster, 1956), both of Middle Cambrian age in Utah. In eastern North America, six species have been described from the Kinzers Formation in Pennsylvania (Resser, 1929; Resser and Howell, 1938) and two species from the Parker Shale in Vermont (Resser and Howell, 1938), all of Early Cambrian age; one species from the Rogersville Shale of Middle Cambrian age in Tennessee (Resser, 1938); and two species from the Nolichucky Formation of Late Cambrian age in Alabama (Resser, 1938).

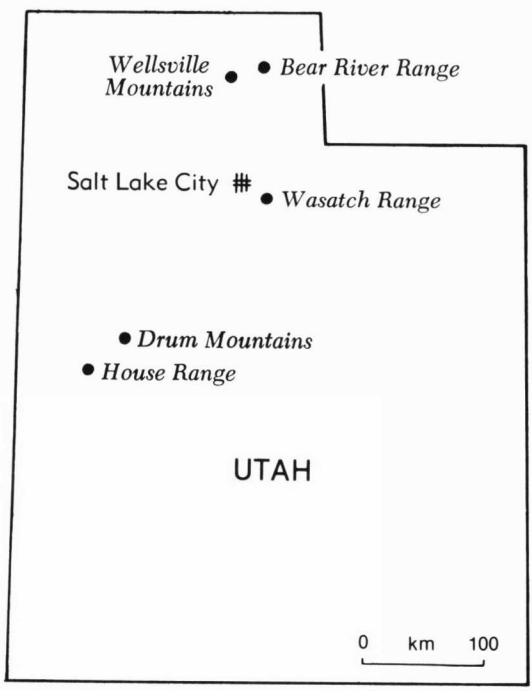

Fig. 1. Areas in Utah from which larger bivalve arthropods of Middle Cambrian age have been collected.

From studies of Burgess Shale specimens that are preserved with soft parts and appendages, Briggs (1976, 1977, 1978) has demonstrated that morphologically very different arthropod bodies may possess quite similar bivalve carapaces. With only the carapace it may be difficult, if not impossible, to distinguish representatives of families of phyllocarid Malacostraca from those of the Protocarididae, which show closest affinities with the Branchiopoda (Briggs, 1976, p. 12). Because soft parts and appendages are not preserved with carapaces of any known bivalve arthropod from the Cambrian of Utah, generic identifications for some specimens are questionable. Also, the family, order, and even class assignments are uncertain for most. Nevertheless, we believe that these specimens warrant description because they provide important information about the distribution and species diversity of a poorly known element of the Cambrian fauna.

Trilobites are the most abundant invertebrate fossils in most Cambrian strata, partly at least because many trilobites possessed a well-calcified dorsal exoskeleton with a high potential for preservation. Evidence from the exceptionally preserved fauna of the Burgess Shale indicates that species of nontrilobite arthropods actually outnumber those of trilobites by more than two to one, and individuals of some species are far more common than those of trilobites (Conway Morris, 1979; Conway Morris and Whittington, 1979; Whittington, 1980). Moreover, preliminary comparison of total numbers and proportions of normally preserved genera from different formations suggests that composition of the biota of the Burgess Shale, rather than being unusual, is probably representative of Middle Cambrian, low-latitude, open-shelf environments in North America (Conway Morris and Robison, 1982). The assemblages of rarely preserved, larger bivalve arthropods in the Middle Cambrian of Utah also bear strong resemblances to the assemblage in the Burgess Shale. This further supports the notion of normality for the Burgess biota.

Stratigraphy.—In general, lithostratigraphic nomenclature in this paper conforms to the usage of Oriel and Armstrong (1971) for northern Utah and Hintze and Robison (1975) for west-central Utah.

The total observed stratigraphic ranges for all species of larger bivalve arthropods presently known from Cambrian strata in Utah are plotted on Figure 2. Relevant biofacies relationships and biostratigraphic nomenclature have been discussed by Robison (1976, 1982).

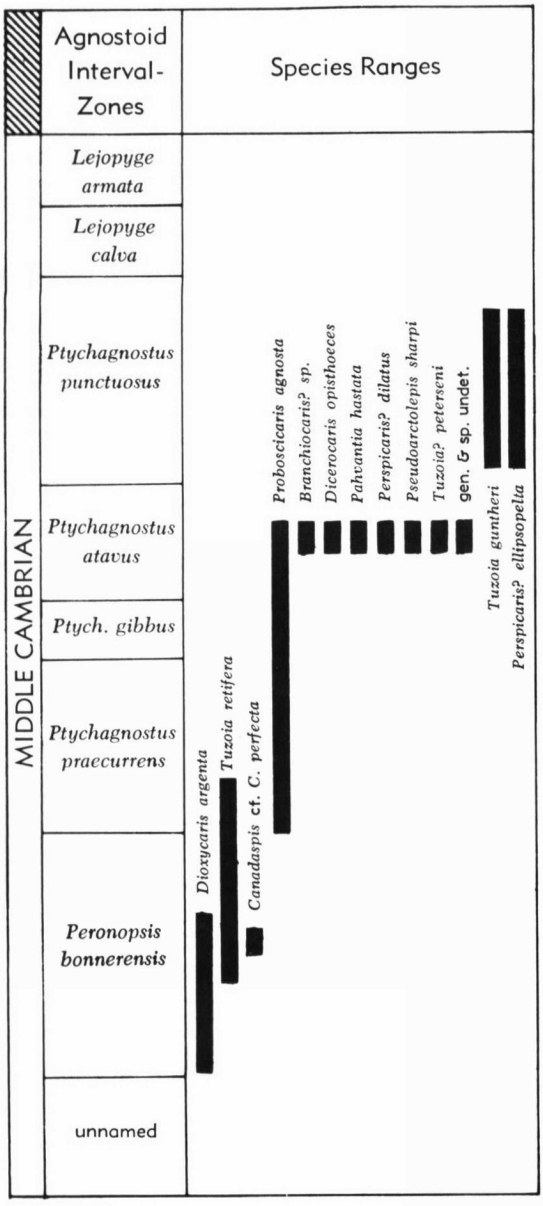

Fig. 2. Observed stratigraphic ranges of larger bivalve arthropods from the Middle Cambrian of Utah. Also included is the probable arthropod *Pahvantia hastata*, new genus and new species.

Localities.—The majority of specimens described here are from four localities. These are listed below and are referred to by number in the section on Systematic Descriptions. Nontrilobite arthropods are not common at any of these localities. Usually a collector will be fortunate to find one such arthropod for every several thousand trilobites. Several other localities have yielded only one or a few specimens of a single species. These less productive localities are described under the "Occurrence" of relevant species in the Systematic Descriptions. All localities are within the mountains or ranges plotted on Figure 1.

114. Medium-dark-gray, laminated, calcareous mudstone in the uppermost 3 m of the Wheeler Formation on a north-trending ridge crest; sec. 24 (unsurveyed), T. 16 S., R. 13 W.; about 700 m south of a stock-watering trough that is supplied by water piped from Swasey Spring on the east side of the House Range.
115. Medium- to dark-gray, calcareous mudstone in the uppermost 30 m of the Wheeler Formation at its type locality in Wheeler Amphitheater; SE¼ sec. 2, T. 17 S., R. 13 W.; central House Range.
716. A 60-m unit of yellowish-gray to grayish-orange calcareous mudstone in the upper Marjum Formation; exposed in ledges along the south side of a large dry wash in the SW¼NW¼ sec. 24 (unsurveyed), T. 17 S., R. 13 W.; about 4 km due south of Wheeler Amphitheater in the central House Range. The stratigraphic position of this mudstone unit has not been precisely determined; however, its basal beds are probably about 300 m above the base of the Marjum Formation.
745. Brown-weathering, dark-gray, laminated, lime mudstone about 180 to 200 m above the base of the Marjum Formation; SW¼SE¼ sec. 13 (unsurveyed), T. 18 S., R. 13 W.; east side of Bird Canyon, House Range.

Repositories.—Most of the specimens described or illustrated in this paper are in the Museum of Invertebrate Paleontology, University of Kansas (KUMIP). A few specimens, including the holotype of *Dioxycaris argenta* (Walcott), are in collections of the U.S. National Museum of Natural History (USNM), Washington, D.C. A few unillustrated specimens are in the collections of Brigham Young University, Provo, Utah, and others are in the private collection of Lloyd Gunther, Brigham City, Utah.

Acknowledgments.—Without the generous

contributions and support of several persons, this study would be far less complete. Exceptional contributions were made by Lloyd, Metta, and Val Gunther of Brigham City, Utah, and R. L. Harris of Delta, Utah. Other important contributions of material were made by L. F. Hintze and M. S. Petersen of Brigham Young University; R. F. Kohl of Willows, California; W. L. Stokes of the University of Utah; and D. C. Kopaska-Merkel and G. R. Vorwald of the University of Kansas. Michael Frederick aided with photography, R. B. Williams prepared the figures, and Virginia Ashlock, D. E. G. Briggs, K. E. Caster, and A. J. Rowell critically reviewed an early draft of the manuscript. This study was supported by National Science Foundation grant EAR-7708689 and the Wallace E. Pratt Research Fund, which is provided to the University of Kansas by the Exxon USA Foundation.

SYSTEMATIC DESCRIPTIONS

Class MALACOSTRACA Latreille, 1806
Subclass PHYLLOCARIDA Packard, 1879
Order CANADASPIDIDA Novozhilov in Orlov, 1960
Family CANADASPIDIDAE Novozhilov in Orlov, 1960

Genus CANADASPIS Novozhilov in Orlov, 1960

Type species.—*Hymenocaris perfecta* Walcott, 1912a, p. 183.

The revised generic diagnosis of Briggs (1978, p. 447) is followed here.

CANADASPIS cf. C. PERFECTA
(Walcott, 1912a)

Plate 1, figures 1-3

For synonymy of *C. perfecta,* see Briggs (1978, p. 448-449).

Description.—Valves ovoid with rather marked posteroventral expansion; hinge line straight, antero- and posterodorsal processes mostly absent; antero- and posterodorsal angles 115 to 120°; free margins lacking spines. Adductor-muscle scar not evident. One valve in places showing narrow border. Observed maximum length ranging from 28 to 39 mm, maximum height from 16 to 25 mm.

Discussion.—Features of these valves, including average size, agree well with those of *C. perfecta* described or illustrated by Briggs, (1978). Although the antero- and posterolateral angles of *C. perfecta* were reported by Briggs (p. 457) to be about 125° and 130°, respectively, some of his illustrations (e.g., fig. 87) show valves with posterodorsal angles as low as about 115°. Thus, the valves from Utah have dorsal angles within the range of those from British Columbia; however, average angle for the few valves from Utah may be smaller.

Valves from the Wheeler Formation of west-central Utah that were previously identified as *Canadaspis?* sp. (Robison, 1971, p. 797) are reassigned here to the new species *Perspicaris? dilatus.* Valves of *C.* cf. *C. perfecta* closely resemble those of *P.? dilatus,* and differences are reviewed in the discussion of *P.? dilatus.*

Occurrence.—Four disarticulated valves (KUMIP 144401, 153893-153895) are preserved in dark-gray, noncalcareous shale from an interval about 23 to 30 m below the top of the Spence Tongue of the Lead Bell Shale on the south side of Antimony Canyon. One articulated carapace (KUMIP 153896) is from an unknown stratigraphic level in the Spence Tongue in Miners Hollow. Both localities are on the west side of the Wellsville Mountains (Fig. 1). All specimens are from the *Peronopsis bonnerensis* Zone (Fig. 2).

Family PERSPICARIDIDAE Briggs, 1978

Genus PERSPICARIS Briggs, 1977

Type species.—*Canadaspis dictynna* Simonetta and Delle Cave, 1975, p. 12.

The generic diagnosis of Briggs (1977, p. 597) is followed here.

PERSPICARIS? DILATUS, n. sp.

Plate 1, figure 4; Plate 2, figures 5-7

Canadaspis? sp. Robison, 1971, p. 797.

Etymology.—Latin *dilatus,* expanded; in reference to the moderate posteroventral expansion of the valves.

Holotype.—Right valve, KUMIP 135128 (Pl. 1, fig. 4), from locality 115, House Range.

Description.—Valves subtrapeziform with moderate posteroventral expansion; maximum

height usually about one-third length from posterior margin. Hinge line normally straight. Antero- and posterodorsal processes usually weakly developed but seemingly broken or not preserved on some specimens; angles generally between 100° and 110°, rarely ranging from about 95 to 115°. Small adductor-muscle scar commonly visible on interior surface of valve; situated anterodorsally with distance from hinge line almost twice that from anterior margin. Free margins lacking spines. Observed maximum length of valve ranging from 29 to 55 mm, maximum height from 18 to 34 mm.

Discussion.—Of the two previously described species of *Perspicaris,* valves of *P.? dilatus* most closely resemble those of *P. dictynna* (Simonetta and Delle Cave, 1975) as described by Briggs (1977); however, valves of *P.? dilatus* are almost four times greater in average size. They also have a more anteriorly situated adductor-muscle scar, usually a better developed posterodorsal process, and no evidence of an original border. Valves of *P.? dilatus* are similar in average size to those of *P. recondita* Briggs (1977) but differ otherwise by having a straight hinge line, smaller antero- and posterodorsal angles, a less strongly curved anterior margin, and an adductor-muscle scar positioned closer to the anterior margin.

Valves of *P.? dilatus* may be difficult to distinguish from those of *Canadaspis* cf. *C. perfecta.* Generally, however, maximum height relative to maximum length is less in *P.? dilatus,* and the antero- and posterodorsal angles are smaller. Although weak, the antero- and posterodorsal processes are usually better developed in *P.? dilatus.* Also, adductor-muscle scars are commonly seen on valves of *P. dilatus* but are not evident on valves of *C.* cf. *C. perfecta.*

Occurrence.—Seven valves (KUMIP 135128-135133, 153899) are preserved in medium-light-gray to dark-gray calcareous mudstone from the upper 30 m of the Wheeler Formation at locality 115 in the House Range. Another nearly complete valve (KUMIP 134189) is in pale-brown noncalcareous mudstone from about 75 m above the base of the Hodges Shale Member of the Bloomington Formation on the south side of Baker Canyon in the Wellsville Mountains. The Wheeler specimens are from the *Ptychagnostus atavus* Zone (Fig. 2), as is probably also the Bloomington specimen.

PERSPICARIS? ELLIPSOPELTA, n. sp.

Plate 2, figures 1-4

Etymology.—Latin *ellipsis,* ellipse; *pelta,* shield. In reference to the elliptical shape of the valves.

Holotype.—Right valve, KUMIP 153902 (Pl. 2, fig. 1), from locality 716.

Description.—Valves elliptical in outline, usually with maximum height only slightly posterior from center, giving an aspect approaching symmetry. Hinge line normally having slight dorsal convexity. Antero- and posterodorsal processes weak or absent; angles ranging from about 110 to 115°. Hinge-line embayments on articulated carapaces of subequal depth. Adductor-muscle scar not evident and free margins lacking spines. Observed maximum length of valve 36 to 71 mm, maximum height 20 to 40 m.

Discussion.—Valves of *P.? ellipsopelta* are characterized by a near uniform convexity of the ventral margin and normally a slight convexity of the hinge line. They further differ from those of *P.? dilatus* by usually having slightly smaller antero- and posterodorsal angles and a somewhat larger average size.

Among more obvious differences, the valves of *P.? ellipsopelta* are on the average at least five times larger than those of *P. dictynna,* have a convex rather than a straight hinge line, and have better developed antero- and posterodorsal processes. Valves of *P.? ellipsopelta* differ from those of *P. recondita* by having smaller antero- and posterodorsal angles, less strongly curved anterior and posterior margins, and a somewhat larger average size.

Occurrence.—Twelve disarticulated valves and three carapaces (KUMIP 153902-153910, 153924-153929) are from locality 716 in the Marjum Formation. Two additional carapaces (KUMIP 159155, 159156) are in brown shale from about 60 m above the base of the Marjum Formation in the SE¼SE¼ sec. 4 (unsurveyed), T. 18 S., R. 13 W. All specimens are from the *Ptychagnostus punctuosus* Zone (Fig. 2) in the House Range (Fig. 1) and were collected by Lloyd and Metta Gunther.

Class and order uncertain
Family PROTOCARIDIDAE Miller, 1889
Genus BRANCHIOCARIS Briggs, 1976
BRANCHIOCARIS? sp.

Plate 1, figures 5, 6

Diagnosis.—Valves subelliptical in outline with slight expansion in inferred anteroventral direction; maximum height slightly anterior from center. Hinge line straight or having slight dorsal convexity. Antero- and posterodorsal processes of moderate size; angles approximately 115°. Adductor-muscle scars and surface reticulation not evident. Free margin nonspinose. Maximum length and height of one valve 56? and 38 mm, respectively; another 30? and 20 mm.

Discussion.—Two nearly complete valves from the Drum Mountains differ in form from all others in the collections from Utah. With a combination of moderate-sized hinge processes and relatively large maximum height compared to maximum length, they most closely resemble species previously assigned to *Branchiocaris* and *Tuzoia;* however, they clearly differ from representatives of *Tuzoia* by lacking marginal spines and surface reticulation. Thus, the two specimens possibly represent *Branchiocaris,* but the available material is inadequate for positive identification.

Because adductor-muscle scars are not evident on the two valves, it is not possible to determine anterior margins with certainty. Evidence of such scars on future discoveries could be taxonomically useful because *Branchiocaris* seems to be the only described Cambrian genus with short ovoid valves that expand anteroventrally.

Occurrence.—Two disarticulated valves (KUMIP 153897, 153898) have been collected by Lloyd Gunther from pale-yellowish-brown, calcareous mudstone of the uppermost 50 m of the Wheeler Formation; NE¼NW¼ sec. 20, T. 15 S., R. 10 W.; Drum Mountains (Fig. 1). Both are from the *Ptychagnostus atavus* Zone (Fig. 2).

Family uncertain

Until details of the soft parts and appendages are known for such genera as *Dicerocaris, Dioxycaris, Isoxys, Proboscicaris, Pseudoarctolepis,* and *Tuzoia,* assignments to families have little meaning. For recent discussions of possible affinities and classification, see Briggs (1976, p. 14) and Glaessner (1979, p. 24-25).

Genus DICEROCARIS, new

Type species.—*Dicerocaris opisthoeces,* n. sp.

Etymology.—Greek *dikeros,* two-horned and *karis,* shrimp; in reference to the pair of hornlike spines on the anterodorsal parts of the carapace.

Description.—Carapace bivalve with hinge line; each valve with a moderately large spine projecting upward and slightly forward from anterodorsal areas. Valves subelliptical with minor posteroventral expansion; anterodorsal process small; posterodorsal corner produced into large process projecting straight back.

Discussion.—Carapaces of *Dicerocaris* differ from those of all other genera of larger bivalve arthropods by the presence of the two large, closely spaced spines on opposite sides of the anterior hinge line. The combination of small anterodorsal process and large posterodorsal process is also distinctive.

Of the Cambrian genera with ovate or subelliptical valves, only *Dicerocaris, Isoxys,* and *Silesicaris* are always longest at the hinge line rather than lower on the valves. In addition to the anterodorsal spine and small anterodorsal process, valves of *Dicerocaris* further differ from those of *Isoxys* and *Silesicaris* by having relatively greater height with less broadly rounded antero- and posteroventral margins.

In valve outline, representatives of *Dicerocaris* resemble those of *Dioxycaris, Pseudoarctolepis,* and *Tuzoia;* however, in addition to differences in spine morphology, valves of *Dicerocaris* have smaller anterodorsal processes.

Dicerocaris is a monotypic genus that presently is known only from the late Middle Cambrian (*Ptychagnostus atavus* Zone) of Utah.

DICEROCARIS OPISTHOECES, n. sp.

Plate 3, figures 1-3

Etymology.—Greek *opisthoekes,* pointed in back; in reference to the large posterodorsal process.

Holotype.—Carapace preserved in lateral aspect with valves slightly offset and rotated, KUMIP 134939 (Pl. 3, figs. 1a, b); from local-

ity 115, House Range.

Description.—Hinge line straight in lateral view. Maximum valve height behind midpoint of valve. Anterodorsal angle approximately 125°, posterodorsal angle between 90° and 95°. Length of hornlike spine near anterodorsal corner of valve approximately one-third maximum valve height. Observed maximum length of valve below hinge line ranging from about 15 to 19 mm; maximum height ranging from about 11 to 15 mm. Observed maximum length of hinge line about 23 mm. Adductor-muscle scar and surface reticulation not evident.

Discussion.—Valves of *D. opisthoeces* are characterized by the moderately large anterodorsal spine, the large posterodorsal process, a relatively long hinge line, and a relatively small posterodorsal angle. No described species has a similar combination of characters.

Although the valves assigned to *D. opisthoeces* are relatively small, they do not seem to represent early instars of another species. As demonstrated by a wide range in size, associated specimens of *Pseudoarctolepis sharpi* show little change in valve form during ontogeny. If *D. opisthoeces* underwent similar ontogenetic development, larger valves could still be easily discriminated from all other species described here.

Because attachment of the anterodorsal spine in *D. opisthoeces* is slightly abaxial from the hinge line, the spine commonly remains covered by a thin veneer of matrix. This usually requires careful removal before the spine can be seen.

On the holotype carapace, the spine on the left valve projects upward and slightly forward (Pl. 3, fig. 1b), apparently in normal position. On the right valve (Pl. 3, fig. 1a), cuticle around the base of the spine has been broken and the spine is rotated so that it projects obliquely backwards. Spines and associated cuticle on the two single valves have been similarly deformed (Pl. 3, fig. 2a, 3). This seemingly altered orientation of spines is such that it is difficult to explain as the result of taphonomic compaction. Perhaps it resulted from escape activities during ecdysis. A random distribution of disarticulated trilobite sclerites in matrix between valves of the holotype carapace suggests that the body was missing (possibly because of ecdysis) at the time of burial.

Occurrence.—One carapace and one disarticulated valve (KUMIP 134939, 134940) were collected by R. L. Harris and Lloyd Gunther, respectively, from the upper 30 m of the Wheeler Formation at locality 115, House Range. Another valve (KUMIP 153900) was collected by G. R. Vorwald from 29 m below the top of the Wheeler Formation in the SE¼SW¼ sec. 21, T. 15 S., R. 10 W., Drum Mountains (Fig. 1). All three specimens are preserved in medium- to dark-gray calcareous mudstone. All are from the *Ptychagnostus atavus* Zone (Fig. 2).

Genus DIOXYCARIS Gürich, 1929

Dioxycaris Gürich, 1929, p. 36; Rolfe, 1969, p. R325; Briggs, 1976, p. 13.
Dyoxycaris Krestovnikov, 1961, p. 5.

Type species.—*Leperditia? argenta* Walcott, 1886, p. 146-147.

Diagnosis.—Carapace bivalve with hinge line. Valves subelliptical with slight posteroventral expansion; anterodorsal process of moderate size, posterodorsal process large; lateral surfaces and free margins lacking spines.

Discussion.—As demonstrated in this paper, the carapaces of *Dioxycaris* Gürich, 1929, and *Pseudoarctolepis* Brooks and Caster, 1956, are remarkably similar except that *Dioxycaris* seems to lack a pair of prominent lateral spines. Few specimens of *Dioxycaris* have been collected and all are poorly preserved. Thus, it is possible that the absence of lateral spines is the result of inadequate preservation and the two genera may be synonyms. Nevertheless, until incomplete preservation of spines is actually demonstrated for *Dioxycaris*, we provisionally recognize both names as being valid.

As presently defined, carapaces of *Dioxycaris* differ from those of *Pseudoarctolepis* by the absence of a pair of large lateral spines. *Dioxycaris* differs from *Branchiocaris, Canadaspis,* and *Perspicaris* by having larger terminal hinge processes, particularly on the posterior end. To date, *D. argenta* is the only species that has been assigned to *Dioxycaris*.

DIOXYCARIS ARGENTA (Walcott), 1886

Plate 3, figures 4-6

Leperditia? argenta Walcott, 1886, p. 146-147, pl. 8, fig. 5.

Dioxycaris argenta (Walcott) Gürich, 1929, p. 36, text-fig. 1.3; Briggs, 1976, p. 13-14, pl. 6, figs. 3, 4 (see for additional synonymy).
Tuzoi argenta (Walcott) Resser, 1938, p. 25.

Holotype.—Probable right valve, USNM 15401 (Pl. 3, fig. 4).

Diagnosis.—Hinge line straight in lateral view. Maximum height of valve at about one-third length from posterior margin. Anterodorsal angle between 105° and 110°, posterodorsal angle between 110° and 115°. Narrow border adjacent to free margins probably adventitious, resulting from taphonomic compaction. Observed maximum length of valve ranging up to 62 mm. Maximum height (30 mm) of longest valve (Pl. 3, fig. 5) probably reduced by taphonomic wrinkling of ventral valve margin.

Discussion.—Valves of *Dioxycaris argenta* most closely resemble those of *Pseudoarctolepis sharpi* but lack a pair of large lateral spines. These species also differ slightly in their antero- and posterodorsal angles, which average about five degrees greater in *D. argenta*. The much higher percentage of disarticulated valves in *D. argenta* than in *P. sharpi* suggests a weaker connection along the hinge. It also could indicate the deposition of remains of *D. argenta* under higher energy conditions; however, both species are commonly associated with articulated trilobites and eocrinoids, suggesting little difference in energy conditions at the times of burial.

Valves here assigned to *D. argenta* vary moderately in maximum height relative to maximum length. The range of variation, however, is no greater than that shown by specimens of *P. sharpi* in which better preservation allows the conclusion that much of the variation resulted from taphonomic deformation of the ventral valve margin. Thus, lacking well-preserved material, we can attach little taxonomic significance to shape of the ventral margin or to ratios based on maximum height.

Without explanation, Resser (1938, p. 25) reassigned *D. argenta* to *Tuzoia*. Valves of *Tuzoia* can be readily differentiated from those of *Dioxycaris* by such features as a lateral carina and spines on the posterior margin. Representatives of *D. argenta* lack these and other features that might support Resser's taxonomic reassignment.

Occurrence.—The holotype of *D. argenta* is from a unit that is presently recognized as the lower member of the Ophir Shale. One of us (R.A.R.) has searched without success for additional topotype specimens of *D. argenta* and concludes that the holotype locality now is probably covered by Utah Highway 152 on the north side of Big Cottonwood Canyon in the Wasatch Range (Fig. 1). The early mining town of Argenta to which Walcott (1886, p. 147) referred, and for which *D. argenta* is named, no longer exists.

According to Walcott (1912b, p. 189), the holotype was associated with *Bathyuriscus productus* (= *Glossopleura producta;* see Palmer, 1954, p. 67) and other taxa. That fauna is presently considered to represent the *Glossopleura* Assemblage-zone of early Middle Cambrian age (the *Glossopleura* Zone is temporally equivalent to part of the *Peronopsis bonnerensis* Zone, Fig. 2). Gürich (1929) and some subsequent authors erroneously indicated that the holotype is from Lower Cambrian strata, whereas Brooks and Caster (1956) erroneously indicated that it is from the House Range (see summary by Briggs, 1976, p. 13).

Additional specimens that we tentatively assign to *D. argenta* include three valves (KUMIP 135145-135147) from about 3 m below the top of the Spence Tongue of the Lead Bell Shale on the south side of Antimony Canyon and one valve (KUMIP 153911) from near the base of the Ute Formation on the north side of Hansen Canyon; all collected by Lloyd and Val Gunther from the west side of the Wellsville Mountains (Fig. 1), and all from the *Glossopleura* Assemblage-zone. Other specimens that possibly represent *D. argenta* are one valve and some fragments (USNM 56513) from the Ute Formation (USNM locality 54a; Walcott, 1912b, p. 151, 202) in Blacksmith Fork Canyon of the Bear River Range (Fig. 1).

Genus PROBOSCICARIS Rolfe, 1962

Proboscicaris Rolfe, 1962, p. 2; 1969, p. R327.

Type species.—*Proboscicaris agnosta* Rolfe, 1969, p. 2-4.

Diagnosis.—Carapace valves subtrapezoidal to subovate and nonspinose. Inferred anterodorsal area commonly produced into large spatulate process.

Discussion.—Valves representing *Proboscicaris* are unusually variable in lateral outline.

Nevertheless, the general form, commonly characterized by a prominent spatulate process, is unique among the larger bivalve arthropod genera of Cambrian age.

Three species of *Proboscicaris* have previously been described. All are from the Burgess Shale. *P. agnosta* Rolfe, 1962, is based on two particularly large valves with relatively small anterodorsal processes, whereas *P. obtusa* Simonetta and Delle Cave, 1975, is based on a single valve with a "wider," more obtuse posterodorsal region and "obsolete" anterodorsal corner. Rolfe (1962, p. 6) mentioned the possibility that "*P. ingens* is simply an older instar of *P. agnosta,*" but further noted that "such radical changes in shape are not common except in early ontogeny." Because no combination of characters readily distinguishes the type specimens of *P. ingens* and *P. obtusa* from the several variable specimens that have been assigned to *P. agnosta* (Rolfe, 1962, fig. 1), we consider all of these to represent a variable population of a single species.

To date, *Proboscicaris* is known from Canada (British Columbia) and the United States (Utah). It has an observed stratigraphic range through part of the lower Middle Cambrian (*Ptychagnostus praecurrens* to *Ptychagnostus atavus* zones).

PROBOSCICARIS AGNOSTA Rolfe, 1962

Plate 4, figure 1

Proboscicaris agnosta Rolfe, 1962, p. 2-4, Pl. 1, figs. 1, 2, text-fig. 1; 1969, Fig. 150.7; Simonetta and Delle Cave, 1975, p. 8, Pl. 6, fig. 1, Pl. 37, figs. 1, 5.

Proboscicaris ingens Rolfe, 1962, p. 4-6, Pl. 1, fig. 3, text-fig. 2; Simonetta and Delle Cave, 1975, p. 8.

Proboscicaris obtusa Simonetta and Delle Cave, 1975, p. 8-9, Pl. 6, fig. 2, Pl. 47, fig. 5.

Diagnosis.—Valves elongate, usually with large, spatulate anterodorsal process. Hinge line slightly concave to slightly convex. Posterodorsal angle obtuse and usually rounded. Ventral margin concave in anterior part and convex in posterior part. Posterior margin commonly with minor indentation in middle or lower part. Surface rarely bearing patches of fine reticulate ridges.

Discussion.—A single specimen from Utah seemingly represents a carapace that has undergone selective dissolution, leaving a thin internal mold. It has a maximum length of 59 mm and a maximum height of 29 mm. Although relatively small, it has an outline that fits well within the range of variation illustrated by Rolfe (1962, text-fig. 1) for valves of *P. agnosta* from the type locality in British Columbia. Compared to the several valves illustrated by Rolfe, the specimen from Utah most closely resembles USNM 139875, differing mainly by its slightly convex rather than slightly concave hinge line and a more angular posterodorsal corner. We do not consider these minor morphological differences to be sufficient to warrant taxonomic separation.

An unusual color pattern renders the Utah specimen difficult to photograph. The spatulate anterior end is light gray with a bleached aspect. A large central area is light brown and a crescentic area at the posterior end is grayish black. The matrix is a pale yellowish-brown, calcareous mudstone. We suggest that the dark posterior deposit may represent carbonaceous residue from decomposition of body tissues.

Occurrence.—One specimen (KUMIP 153901) was collected by Lloyd Gunther from the upper 30 m of the Wheeler Formation in the SE¼SE¼NE¼ sec. 35 (unsurveyed), T. 17 S., R. 13 W. in the central House Range (Fig. 1).

The discovery of *P. agnosta* in Utah extends the observed stratigraphic range of the species upward from the *Ptychagnostus praecurrens* Zone to the *Ptychagnostus atavus* Zone (Fig. 2). It also extends the observed geographic range from British Columbia to Utah.

Genus PSEUDOARCTOLEPIS Brooks and Caster, 1956

Pseudoarctolepis Brooks and Caster, 1956, p. 10; Rolfe, 1969, p. R327.

Type species.—*Pseudoarctolepis sharpi* Brooks and Caster, 1956, p. 11-12.

Diagnosis.—Carapace bivalve with hinge line. Valves subelliptical with slight posteroventral expansion; large, long, posteriorly curved spine projecting from anteromedian region; anterodorsal process of moderate size, posterodorsal process large; free margins lacking spines. Rostrum absent.

Discussion.—The most distinctive feature of *Pseudoarctolepis* is the pair of prominent lateral spines. These give the carapace a superficial resemblance to the cephalothoracic dermal armor of some Devonian arthrodire fish; however, composition, structure and various morphologic details indicate an arthropod affinity.

Previously, the taxonomic concept of *Pseudoarctolepis* was based solely on the holotype of *P. sharpi,* which is an articulated carapace that is preserved in parallel aspect. Previous authors have failed to recognize that approximately the lower half of each valve is folded beneath the exposed dorsal carapace. This fact resulted in an erroneous restoration of original valve form, which is corrected in the following review of *P. sharpi.*

The possibility that *Pseudoarctolepis* is a junior synonym of *Dioxycaris* is reviewed in the discussion of *Dioxycaris.*

PSEUDOARCTOLEPIS SHARPI
Brooks and Caster, 1956

Plate 4, figures 3-5; Plate 5, figures 1-6; Plate 6, figures 1, 2

Pseudoarctolepis sharpi Brooks and Caster, 1956, p. 11-12, Pl. 2 and text-fig. 1.1,2.

Material.—The holotype, which has been contributed to the University of Kansas Museum of Invertebrate Paleontology (KUMIP 159141; Pl. 5, fig. 6) by Prof. W. L. Stokes, is an articulated carapace preserved in parallel aspect. Collecting by several persons during the past two decades has produced an additional 23 articulated carapaces preserved in parallel aspect, 3 carapaces preserved in lateral aspect, and 16 disarticulated valves preserved in lateral aspect. These additional specimens are now in collections at the University of Kansas (KUMIP 135134-135142, 144383-144385, 144396-144398, 153912-153916, 159142-159153), Smithsonian Institution (USNM 159918), and Brigham Young University (unnumbered specimens), and in the private collection of Lloyd Gunther.

Diagnosis.—Hinge line straight or slightly convex upward in lateral view. Maximum valve height at about one-third length from posterior margin. Anterodorsal angle usually between 110° and 115°, posterodorsal angle usually between 115° and 120°. Adductor-muscle scar not evident on laterally compressed valves but site coinciding with small deformed area in anterodorsal region on some dorsoventrally compressed valves (see Pl. 5, fig. 6). Large, posteriorly curved spine attached just above midheight of valve and about one-third of length from anterior margin; length of spine ranging from about one-fourth to one-third that of valve. Surface of valves smooth except for wrinkles and folds seemingly caused by taphonomic compaction.

Discussion.—Specimens of *P. sharpi* are preserved as dark carbonaceous films in calcareous mudstone. All show effects of deformation related to compaction, which suggests that the original carapace was thin and not mineralized. Lack of decalcification in associated trilobites and echinoderms further supports this suggestion.

When an articulated carapace of *P. sharpi* came to rest on the seafloor, the projecting lateral spines normally would have prevented the carapace from resting on its sides. This seemingly is why most articulated carapaces are preserved in parallel aspect. Also, as the result of dorsoventral compaction in mud, approximately the lower half of each valve is usually folded underneath or crumpled beneath the upper half. This latter condition in the holotype was not recognized by Brooks and Caster (1956, text-fig. 1.2), who illustrated a restoration in lateral view of a relatively long, anteroventrally expanded valve with the large lateral spine attached near the ventral margin. New specimens, several with nonfolded valves (e.g., Pl. 5, figs. 2-4), demonstrate a relatively greater valve height than originally described. Moreover, the lateral spine is actually attached at about midheight on the valve (Pl. 4, fig. 3; Pl. 5, fig. 3) and the valve expands slightly in a posteroventral direction (Pl. 5, figs. 3,4).

Style of carapace deformation in *P. sharpi* provides additional information about morphology as well as clues to the attitude of carapaces at the time of their burial. For example, noticeably more surface area of either one or the other valve is exposed in articulated carapaces that are preserved in parallel aspect (e.g., Pl. 6, fig. 1). This probably resulted from the carapaces being tilted on the seafloor at the time of burial, each resting on the ventral margin and spine tip of either one or the other of the valves (Fig. 3A). Vertical compaction sub-

sequently caused some parts of the carapace to be flattened while other parts were folded underneath or crumpled in place (Fig. 3B). These differences in area of exposure also indicate that the large lateral spines projected outward at approximately right angles to the valve surfaces (Fig. 3A). Otherwise, if the spines projected downward, the resting carapace would have had less tilt and a more symmetrical preservation; if the spines projected upward, the asymmetry would have been more pronounced.

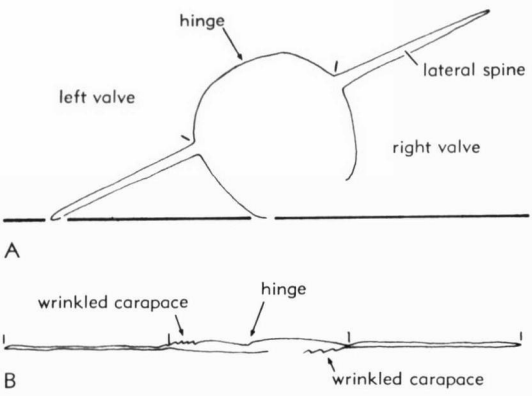

Fig. 3. Effects of compaction on the carapace of *Pseudoarctolepis sharpi*, shown in section through lateral spines. *A*, Carapace resting on tip of left spine and ventral margin of left valve. *B*, After compaction in mud, upper left and lower right parts of valves are crumpled and narrower than upper right and lower left parts.

Where the large lateral spine attached to the carapace wall, the spine has a broad, subtriangular cross section with an obtuse apex on the dorsal surface (Pl. 4, fig. 3). Additional evidence for a dorsal ridge on these spines has not been observed; however, such a ridge may have been obliterated by taphonomic compaction.

An indication of original valve convexity is provided by articulated carapaces of *P. sharpi* that are preserved in parallel aspect with the lower parts of their valves folded underneath the upper parts (e.g., Pl. 5, figs. 5, 6). Maximum width, which may have been slightly accentuated by compaction, is at the position of the lateral spines. The anterior decrease in width is more pronounced than is the posterior decrease.

Single valves preserved in lateral aspect commonly show a zone of wrinkling near the valve margins. On some specimens (Pl. 5, fig. 1), these wrinkles may weakly demarcate a rim or borderlike area; however, the original surface was probably smooth and all such features probably represent nothing more than deformation by compaction of thin, convex valves. Amount of surface wrinkling near the ventral margin of disarticulated valves is particularly variable and has variably altered the original valve height as well as the position of the spine base relative to the ventral margin (cf. Pl. 5, figs. 1-4). Thus, for most valves, original length to height ratios are difficult, if not impossible, to determine. The zone of wrinkling also probably indicates that the lower part of the valve originally had a greater adaxial curvature than did parts above (Fig. 3A).

Two small, broken bulges near the anterior margin of the holotype carapace were considered by Brooks and Caster (1956, p. 10, pl. 2) possibly to "represent the position of compound eyes or more likely, the places of origin of an adductor carapace muscle." Such features are present on other carapaces of *P. sharpi* preserved in parallel aspect, but are not evident on valves preserved in lateral aspect. We concur with the suggestion that they most likely represent insertion sites for adductor muscles, and we have found no evidence for an ocular function. Moreover, the sites seem to have been differentially deformed only during dorsoventral compaction of valves.

Although the carapace is produced anteriorly into a prominent hingeline process, there is no evidence of a separate, movable rostral plate as in some of the Phyllocarida (Rolfe, 1969). An even larger posterior hingeline process is present, and in some specimens these processes are medially torn or cleft (e.g., Pl. 6, fig. 1). As noted by Brooks and Caster (1956), this medial cleft indicates an axis of weakness and articulation rather than a carina.

Available valves of *P. sharpi* range from 20 to approximately 110 mm in maximum length and provide some information about ontogeny. Only one fragmentary valve exceeds 75 mm in length and it is appreciably larger than all others in the collection. Modal length is between 50 and 55 mm (Fig. 4). The smallest specimens (Pl. 4, figs. 2, 4) differ little in lateral valve outline from those in the modal size range. Lateral spines, however, show anisometric growth, increasing from about a third of

the valve length in small specimens (Pl. 4, fig. 2) to more than half in larger specimens (Pl. 4, fig. 5a,b). These lateral spines may have functioned as stabilizers and may indicate a swimming mode of life. The anisometric increase in spine length was probably coordinated with volumetric increase in the body.

P. sharpi remains the only species referable to *Pseudoarctolepis*.

Occurrence.—All specimens of *P. sharpi* were collected from either the upper 40 m of the Wheeler Formation in the House Range or the upper 80 m of the Wheeler Formation in the Drum Mountains (Fig. 1). The specimens are from several localities, the most productive being 114 and 115. All are from the *Ptychagnostus atavus* Zone (Fig. 2).

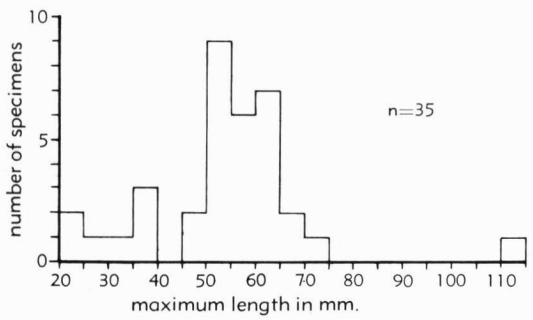

Fig. 4. Observed size distribution in *Pseudoarctolepis sharpi*.

Genus TUZOIA Walcott, 1912

Tuzoia Walcott, 1912a, p. 187; Henriksen, 1928, p. 15; Resser, 1929, p. 6-7; Shimer and Shrock, 1944, p. 655; Brooks and Caster, 1956, p. 13; Öpik, 1968, p. 10; Rolfe, 1969, p. R328; Simonetta and Delle Cave, 1975, p. 7-8; Briggs, 1977, p. 618; Glaessner, 1979, p. 23.

Type species.—*Tuzoia retifera* Walcott, 1912a, p. 187, Pl. 33, fig. 2.

Diagnosis.—Carapace bivalve with hinge line. Valves ovoid, usually with marked posteroventral expansion; lateral ridge commonly extending almost full length of valve at about midheight, rarely vestigial; terminal hinge processes medium to large. Spines variable; none to several along dorsal margin, one to several along posterior margin, rare on ventral margin. Surface normally covered by reticulate pattern of fine ridges; mesh finer on lateral ridge and near valve margins.

Discussion.—Valves of *Tuzoia* differ from those of most other larger bivalve genera of Cambrian age by development of marginal spines and conspicuous surface reticulation. In general outline, excluding spines, valves of *Tuzoia* closely resemble those of *Canadaspis* but have larger terminal hinge processes. The terminal hinge processes of *Tuzoia* closely resemble those of *Dioxycaris* and *Pseudoarctolepis*, but otherwise the posteroventral margin is usually more expanded in *Tuzoia*.

The thin cuticle of *Tuzoia* commonly shows evidence of taphonomic deformation. Also, where several valves are available from a single locality, the number of marginal spines tends to vary. For some specimens, careful preparation has demonstrated that spines may remain buried in matrix. In other specimens, spines have probably been broken off, but this may be difficult, if not impossible, to determine. Outline of valves and spacing of spines may be significantly modified by compression, the principal amount usually depending on orientation of the specimen at the time of its burial. Compression may also obliterate the fine surface reticulation. Some change in spine morphology may have occurred during ontogeny. Thus, all of these possibilities deserve evaluation in discrimination of species of *Tuzoia*.

Spine morphology of the dorsal margin is especially difficult to determine for valves of *Tuzoia*. Where carapaces are preserved in parallel aspect, some show that the hinge line separates closely spaced pairs of spines (e.g., Resser, 1929, Pl. 7, fig. 3). On bedding surfaces where disarticulated valves are mostly preserved in lateral aspect, some or all of the dorsal spines may remain covered by a thin veneer of matrix and their presence may easily go undetected. Consequently, particular care should be exercised in using dorsal spines for taxonomic discrimination.

In most species of *Tuzoia*, a lateral ridge extends nearly the full length of each valve, generally in a central position and parallel to the hinge. Some authors (Resser, 1929, p. 6; Raymond, 1935, p. 228; Rolfe, 1969, p. R328) have interpreted this ridge to be an original feature of the valve. Because of a somewhat variable position, other authors (Simonetta and Delle Cave, 1975, p. 8; Briggs, 1977, p. 620)

have argued that the ridge is a secondary feature resulting from compression. After review of this matter, we conclude that the lateral ridge is a primary feature and that its position is variable because of secondary compression. A primary origin for the ridge is indicated by a major difference in average diameter of reticulae on the ridge and on adjacent valve surfaces, the latter generally being 5 to 10 times greater. Moreover, reticulae on the ridge rarely show evidence of differential deformation. In most species, the largest marginal spine is on a direct line with the lateral ridge, which suggests an original functional relationship. In valves where the lateral ridge is markedly closer to either the dorsal or ventral margin, the surface between commonly shows abnormal wrinkling parallel to the ridge (e.g., Resser, 1929, Pl. 3, fig. 1) or lengthwise stretching of reticulae (e.g., Resser, 1929, Pl. 2, fig. 1). Both of these features indicate secondary differential decrease in height within that part of the valve and a corresponding secondary displacement in position of the lateral ridge.

Henriksen (1928, p. 13) suggested that specimens of *Anomalocaris* may represent a segmented body belonging with carapaces of either *Tuzoia* or *Carnarvonia*. In support of Henriksen's idea, Resser (1929, p. 6) noted that "three of the four localities yielding *Tuzoia* have thus far also furnished *Anomalocaris*." Briggs (1979) has recently given a detailed analysis of *Anomalocaris* and reinterpreted the specimens as ambulatory appendages of an exceptionally large arthropod, probably exceeding one meter in length. A similar conclusion was recorded by Bergström (1979, p. 10-11), who interpreted the specimens of *Anomalocaris* to be possible limbs of a large, uniramian arthropod.

Among the Cambrian genera of larger bivalve arthropods, *Tuzoia* is one of the most common and most widely distributed. It presently has an observed stratigraphic range from the upper Lower Cambrian to the upper Middle Cambrian. Geographically, it is known from Australia (South Australia), Canada (British Columbia), China (Manchuria), and the United States (Pennsylvania, Utah, Vermont).

TUZOIA GUNTHERI, n. sp.

Plate 7, figures 1, 2; Plate 8, figures 4, 5; Plate 9, figure 2

Etymology.—After Lloyd, Metta, and Val Gunther, who have generously contributed many of the specimens on which this study is based.

Holotype.—Left valve, KUMIP 153917 (Pl. 7, fig. 2), from locality 716, House Range.

Description.—Valve commonly with single, short, broad-based, vertical spine on dorsal margin, approximately one-fifth length from anterior end; hinge line, in lateral view, straight to slightly convex behind spine, offset to slightly lower level in front of spine. Anterodorsal process moderate to large, usually pointing straight forward; posterodorsal process long and commonly directed upward and backward at about 45° angle from hinge line. Anterodorsal angle usually between 110° and 115°, posterodorsal angle usually between 108° and 113°. Maximum valve height about two-fifths length from posterior margin. Lateral ridge vestigial; seemingly confined to anterior half of valve, about one-third way down from dorsal margin; indicated mainly by finer pattern of surface reticulation. Posterior margin with 3 or 4 spines of short to moderate length. Observed maximum length of valve, exclusive of spines, to 125 mm and maximum height to 99 mm.

Discussion.—Most of the better preserved valves of *T. guntheri* show only three posterior marginal spines (Pl. 7, fig. 1). The highest and second largest of these is situated at about mid-height on the margin. The smallest spine is in the lowest position, whereas the largest and longest spine is intermediate in position. Rarely, a tiny fourth spine is present about midway along the upper half of the posterior margin (Pl. 7, fig. 2).

The lateral ridge on valves of *T. guntheri* is indicated by only a weak line of finer reticulae on the anterior half of better preserved valves (Pl. 7, fig. 2). As this is the stratigraphically youngest species of *Tuzoia*, and earlier species with short lateral ridges are unknown, a late phyletic reduction of ridge length may be indicated.

In valve outline and surface reticulation, *T. guntheri* most closely resembles *T. retifera* Walcott (1912a) and *T. polleni* Resser (1929); however, *T. guntheri* differs from both by having only a vestigial lateral ridge, which is situated higher on the valve. Consistent differences in spine morphology are also evident. The number of marginal spines in *T. guntheri* is seemingly less variable than in *T. retifera*. Further, in *T. guntheri* the largest and longest

spine is low on the posterior margin and well below the level of the lateral ridge, whereas in *T. retifera* the largest marginal spine is situated at about midheight, directly behind the lateral ridge. Valves of *T. guntheri* further differ from those of *T. polleni* by having a less spinose dorsal margin.

Occurrence.—Three valves (KUMIP 153917, 153919, 153920), including the holotype, have been collected from locality 716. Twenty-two valves and three carapaces (KUMIP 134188, 134790-134798, 144390-144395, 144399, 144400, 144982, 144987-144989, 153918, 153921) have come from locality 745. An additional valve (KUMIP 159154), the largest known, is from about 60 m above the base of the Marjum Formation in the SE¼SE¼ sec. 4 (unsurveyed), T. 18 S., R. 13 W. All specimens are preserved in brown-weathering, laminated, lime mudstone in the Marjum Formation of the House Range (Fig. 1). All are from the *Ptychagnostus punctuosus* Zone (Fig. 2), and most were collected by either Lloyd Gunther, Metta Gunther, Val Gunther, or R. L. Harris.

TUZOIA? PETERSENI, n. sp.

Plate 9, figure 1

Etymology.—After Prof. M. S. Petersen of Brigham Young University, who collected the only known specimen of this unusual species.

Holotype.—Right? valve, KUMIP 134799.

Description.—One relatively small, subpolygonal valve; anterior margin missing. Dorsal margin slightly convex and thickened, perhaps by curling; small, vertical spine at about midlength. Posterodorsal angle about 115°. Posterodorsal corner produced into giant, slightly curved, oblique spine; length approximately equal to maximum valve height. Two similar but successively shorter, irregularly spaced spines arising from upper half of posterior margin. Maximum valve height, exclusive of spines, 10.3 mm.

Discussion.—Although not well preserved, this extraordinary valve possibly warrants assignment to a new genus. It is characterized by three unusually large spines on the posterior margin and a smaller spine on the dorsal margin. Placement of these spines is somewhat similar to that in species of *Tuzoia;* however, the posterior and ventral outlines of the valve differ by being less smoothly curved. Also, the maximum height is near the center of the valve rather than being well back on the posterior half. The cuticle is not well enough preserved to determine the presence or absence of original surface reticulation.

Among *Tuzoia*-like species, only *T.? dunbari* Resser (1929, Pl. 7, fig. 1) has marginal spines as large as those of *T.? peterseni,* but the form and arrangement of spines differ greatly in the two species.

Occurrence.—Upper Wheeler Formation (*Ptychagnostus atavus* Zone) near Marjum Pass, House Range.

TUZOIA RETIFERA Walcott, 1912

Plate 8, figure 3

Tuzoia retifera Walcott, 1912a, p. 187, Pl. 33, fig. 2; Resser, 1929, p. 7-8, Pl. 1, figs. 1, 2, Pl. 4, fig. 3; Gürich, 1929, p. 42, text-fig. 2.4; Shimer and Shrock, 1944, Pl. 278, figs. 15, 16; Simonetta and Delle Cave, 1975, p. 8, Pl. 6, fig. 8, Pl. 46, figs. 3-5, Pl. 47, fig. 1, Pl. 48, figs. 1-4, Pl. 49, fig. 4.

Tuzoia burgessensis Resser, 1929, p. 8, Pl. 2, fig. 1, Pl. 3, fig. 1; Brooks and Caster, 1956, text-fig. 1.5; Rolfe, 1969, Fig. 152.6.

Tuzoia canadensis Resser, 1929, p. 8, Pl. 2, figs. 2, 3.

New material.—One left valve (part and counterpart), KUMIP 153918.

Diagnosis.—Hinge line usually straight. Maximum valve height at about one-third length from posterior margin. Anterodorsal angle usually between 100° and 110°, posterodorsal angle usually between 110° and 115°. Lateral ridge extending almost full length of valve at about midheight. Multiple small spines present in some along dorsal margin. Number and size of spines on posterior margin variable; largest spine normally situated directly behind end of lateral ridge; second largest spine usually posteroventral, third largest spine usually above level of lateral ridge; additional smaller spines may be present, may extend onto ventral margin, and may grade to serrations.

Discussion.—Simonetta and Delle Cave (1975, p. 8) tentatively considered *T. burgessensis* Resser and *T. canadensis* Resser to be junior synonyms of *T. retifera* Walcott. We accept the synonymy of these species and conclude that the characters used by Resser (1929) to define his two species are mainly attributable

to taphonomic compression. Specimens that were assigned to *T. burgessensis* (Resser, 1929, Pl. 2, fig. 1; Pl. 3, fig. 1) are longer than usual but show lengthwise wrinkles, which indicate a postmortem decrease in relative height. One of these (Resser, 1929, Pl. 2, fig. 1) also tapers posteroventrally, seemingly because of postmortem crumpling and gathering of cuticle toward the posterior end of the lateral ridge. This same specimen is the basis for line drawings (Brooks and Caster, 1956, text-fig. 1.5; Rolfe, 1969, fig. 152.6) that convey a misleading image of the normal valve outline in *Tuzoia,* which expands anteroventrally. Specimens that were assigned to *T. canadensis* have additional minor marginal spines that differ in number even in the two specimens illustrated by Resser (1929, Pl. 2, figs. 2, 3). Hence, we attribute this difference in spinosity to intraspecific variation.

A single left valve from Utah fits within the range of morphologic variation shown by specimens from the type locality in British Columbia. Compression has nearly obliterated the long lateral ridge on this valve but the feature is still discernible when viewed under oblique light. Bases of a few small spines are evident along the dorsal margin. Spines on the posterior margin are not well preserved; however, the base of the large spine (on unillustrated counterpart) behind the lateral ridge and most of the large posteroventral spine are evident. In places the fine reticulate ridges on the valve surface are underlain by delicate deposits of pyrite.

Occurrence.—The valve from Utah is preserved in dark-gray, noncalcareous shale. It was collected by Lloyd and Val Gunther from an unknown stratigraphic level in the Spence Tongue of the Lead Bell Shale near the mouth of Donation Canyon on the west side of the Wellsville Mountains (Fig. 1).

The discovery of *T. retifera* in Utah extends the observed stratigraphic range of the species downward from the *Ptychagnostus praecurrens* Interval-zone to the upper *Peronopsis bonnerensis* Interval-zone (Fig. 2). It also extends the observed geographic range from British Columbia to Utah.

Genus and species undetermined

Plate 9, figure 3

Description.—Probable carapace with elongate, subfusiform valves. Margins of valves divided into three parts of unequal length; longest part broadly curved, intermediate and shortest parts nearly straight. Anterior and posterior ends acutely pointed. Surface having microgranular texture.

Discussion.—Two partly superimposed specimens (Pl. 9, fig. 3) appear to represent laterally compressed carapaces of an undetermined arthropod. The moderate-brown cuticle of each specimen is folded along a nearly straight line, forming a margin of intermediate length. Space between the folded valves is filled with very light-gray calcareous mudstone, which thickens away from the folded margin. The long, free margin is broadly curved. The short margin, oblique to the folded margin, is inferred to be posterodorsal. This short margin may have bounded one side of a deep axial embayment of the carapace.

The possibility that these two specimens are folded and dorsoventrally compressed valves of a single carapace has been considered. Such a possibility seems unlikely, however, because of the unusual form. Also, a hinge margin is not obvious.

The Wheeler specimens bear superficial resemblance to carapaces belonging to several members of the phyllocarid orders Leptostraca and Archaeostraca. For example, the general form and relative lengths of the tripartite margins are remarkably similar to those of the extant leptostracan *Nebalia bipes* (Rolfe, 1969, fig. 120). There is also a lesser resemblance to such fossil archaeostracans as *Callizoe bohemica* (Rolfe, 1969, fig. 142.2). Nevertheless, the Wheeler specimens differ from all of these by having much more acute anterior and posterior ends. At this time, the specimens cannot be assigned with confidence to any described genus.

Occurrence.—Wheeler Formation (*Ptychagnostus atavus* Zone) at locality 115, House Range. Associated on the same bedding surface are specimens of the agnostoid trilobite *Peronopsis interstricta* and numerous small shells of a *Helcionella*-like mollusk. The specimens were collected by L. F. Hintze.

Phylum ARTHROPODA?
Class, order, family uncertain
Genus PAHVANTIA, new

Type species.—*Pahvantia hastata,* n. sp.

Etymology.—After the Pahvant Indians of western Utah.

Description.—Carapace univalve or obscurely hinged bivalve, elongate, bilaterally symmetrical, and shaped like a spearhead. Maximum width slightly behind prominent, rounded shoulders and about one-third distance from inferred anterior end. Laterally constricted, shanklike process nearly parallel sided; width less than one-half that of main subtriangular part. Inferred posterior end acutely pointed.

Discussion.—In form, three specimens representing this new genus are unlike the exoskeletal remains of any known arthropod. In details of color, texture, thickness, and mode of preservation, however, they seem to be composed of cuticular material similar to that of associated larger bivalve arthropods. Hence, the genus is questionably assigned to the Arthropoda but further assignment to class, order, and family is deferred.

The relative size, general form, and lack of segmentation suggest that the specimens are cephalothoracic carapaces. If so, bilateral symmetry indicates a complete or nearly complete carapace rather than disarticulated, hinged valves. Inferred anterior and posterior ends are designated with much uncertainty.

Pahvantia is a monotypic genus that presently is known only from the late Middle Cambrian (*Ptychagnostus atavus* Zone) of Utah.

PAHVANTIA HASTATA, n. sp.

Plate 7, figure 3; Plate 8, figures 1, 2

Etymology.—Latin *hastatus,* spear-shaped; in reference to the general similarity to a spearhead, although the inferred anterior and posterior ends are reversed.

Holotype.—Relatively small but seemingly complete or nearly complete carapace, KUMIP 134878 (Pl. 8, fig. 2), from locality 115, House Range.

Description.—Because this is a monotypic genus, description of the species is the same as that of the genus. The holotype is 18 mm wide and 40 mm long. One fragmentary paratype is 42 mm wide and was probably about 85 mm long, the other was probably about 40 mm wide and about 90 mm long.

Discussion.—A feature that may prove to be of taxonomic importance is the terminal margin of the anterior process, which has an angular cleft successively flanked by a pair of small lobes, a pair of shallow rounded indentations, and a pair of small marginal spikes. Another such feature is a pair of weak exsagittal lines that commence at small pointed projections or slight flection points midway out on the shoulders and extend straight back across the outer edges of the main ovate part. These lines may mark the inner edges of subjacent doublures or infolded carapace; however, these possibilities seem unlikely because of the straightness of the lines and the roundness of the lateral margins where folding would have occurred.

Occurrence.—Three specimens of *P. hastata* (KUMIP 134187, 134878, 134879) were collected by R. L. Harris from a quarry in the Wheeler Formation at locality 115, House Range (Fig. 1). They are preserved in dark-gray calcareous mudstone of the *Ptychagnostus atavus* Zone (Fig. 2).

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EXPLANATION OF PLATES

Plate 1

FIGURE

1-3. *Canadaspis* cf. *C. perfecta* (Walcott), all from the Spence Tongue of the Lead Bell Shale, Wellsville Mountains.——*1.* Left valve, ×1.5, KUMIP 153893.——*2.* Right? valve, ×2.0, KUMIP 153894.——*3a,b.* Counterparts of right valve, ×1.5 and 2.0, KUMIP 144401.

4. *Perspicaris? dilatus,* n. sp. Right valve, holotype, from the Wheeler Formation, House Range, ×1.3, KUMIP 135128. Subcircular muscle scar (arrow) shows near anterior margin. Irregular, linear markings were probably made by a burrowing animal after burial of valve. Impressions of small, disarticulated trilobite sclerites are also evident.

5,6. *Branchiocaris?* sp., both from the Wheeler Formation, Drum Mountains.——*5.* Left valve?, ×1.3, KUMIP 153897.——*6.* Incomplete left? valve, ×2.0, KUMIP 153898.

Plate 2

FIGURE

1-4. *Perspicaris? ellipsopelta,* n. sp.; all from the Marjum Formation, House Range.——*1.* Right valve, holotype, ×1.0, KUMIP 153902.——*2.* Left valve, ×1.5, KUMIP 153903.——*3.* Nearly complete carapace preserved in parallel aspect, anterior toward top, ×2.0, KUMIP 153904. Slight dorsal convexity of hinge line together with compression after burial has resulted in slight overlap of dorsal valve margins in central part of hinge line. Maximum height of left valve has been reduced by crumpling in area along ventral margin.——*4.* Left valve, ×1.3, KUMIP 153905.

5-7. *Perspicaris? dilatus,* n. sp.; all from the Wheeler Formation, House Range; all ×1.5.——*5.* Right valve, KUMIP 135131.——*6.* Right valve, KUMIP 135130.——*7.* Left valve, KUMIP 135129.

Plate 3

FIGURE

1-3. *Dicerocaris opisthoeces,* n. gen. and n. sp.; all from the Wheeler Formation and all ×2.5.——*1.* Holotype carapace preserved in lateral aspect with valves slightly offset and rotated; from locality 115, House Range; KUMIP 134939. Disarticulated trilobite sclerites with coatings of cone-in-cone calcite indent surfaces of the carapace. *1a,* Interior view of most of right valve, which is overlain by small anteroventral part of left valve; anterodorsal cuticle of right valve is broken and spine has been rotated obliquely backwards. *1b,* Exterior view of posterior part of right valve and interior view of anterior part of left valve, which seemingly has anterodorsal spine preserved in normal position. ——*2a,b.* Counterparts of right valve with secondarily misoriented anterodorsal spine; from locality 115, House Range; KUMIP 134940.——*3.* Mostly exposed right valve with secondarily misoriented anterodorsal spine; from the SE¼SE¼SW¼ sec. 21, T. 15 S., R. 10 W., Drum Mountains; KUMIP 153900.

4-6. *Dioxycaris argenta* (Walcott).——*4.* Holotype from the lower member of the Ophir Shale, USNM locality 30a in the Wasatch Range, ×1.0, USNM 15401.——*5.* Right? valve from the Spence Tongue of the Lead Bell Shale, Wellsville Mountains, ×1.0, KUMIP 135145.——*6.* Left? valve from the Ute Formation, Wellsville Mountains, ×1.3, KUMIP 153911.

Plate 4

FIGURE

1. *Proboscicaris agnosta* Rolfe.——*1a,b.* Counterparts of a probable thin internal mold from the Wheeler Formation, House Range, both ×1.3, KUMIP 153901.

2-5. *Pseudoarctolepis sharpi* Brooks and Caster; all from the Wheeler Formation, House Range.——*2.* Dorsoventrally compressed juvenile carapace with upper parts of each valve flattened and lower parts folded inward, causing the lower parts to be hidden from view; lateral spines are relatively short; ×2.0, KUMIP 135139.——*3.* Enlarged interior view of lateral spine base showing broad, triangular cross section; same valve as Pl. 5, fig. 3; ×5.0, KUMIP 153912.——*4.* Juvenile carapace with left valve partially flattened parallel to bedding surface and right valve dorsoventrally crumpled; ×2.5, KUMIP 135135.——*5a,b.* Counterparts of dorsoventrally compressed mature carapace with relatively long lateral spines; both ×1.0, KUMIP 153913. Separation along different surfaces has exposed the inward-folded, anterior, lower part of the right valve (upper right, *5a;* upper left, *5b*). A more ex-

tensive surface exposes much of the upper left valve and the posterior upper part of the right valve. The posterior end of the carapace has suffered dorsoventral crumpling.

Plate 5

FIGURE

1-6. *Pseudoarctolepis sharpi* Brooks and Caster, all from the Wheeler Formation, House Range.——*1.* Exterior of right valve with area below lateral spine strongly crumpled; dark spots on adjacent bedding surface may represent remains of the alga *Morania;* × 1.0, KUMIP 153914.——*2.* Interior of left valve, which is overlain by small part of anterior right valve; × 1.3, KUMIP 153915.——*3.* Interior of right valve showing lateral spine base at about 0.3 length from anterior margin (compare Pl. 4, fig. 3); specimen is impressed against sclerites of the trilobites *Elrathia kingii* and *Peronopsis interstricta;* × 1.0, KUMIP 153912.——*4.* Exterior of right valve with minor crumpling of anteroventral region; slightly elevated base of lateral spine about 0.3 length from anterior margin; dark spots on adjacent bedding surface may represent *Morania,* and the broad, lighter colored trace that extends from top to bottom of the figure may represent a burrow or feeding trail of an unknown animal; × 1.0, KUMIP 153916.——*5.* Dorsoventrally compressed carapace with parting surface exposing internal anterodorsal and exterior posteroventral parts of folded valves; associated with *Elrathia kingii;* × 1.3, KUMIP 135142.——*6.* Holotype carapace preserved in parallel aspect with lower parts of valves folded underneath; small pair of broken bulges near anterior margin may be sites where adductor muscles inserted; × 1.0, KUMIP 159141.

Plate 6

FIGURE

1,2. *Pseudoarctolepis sharpi* Brooks and Caster, both from the Wheeler Formation, House Range, and both × 1.0. These two carapaces, each preserved in parallel aspect, differ markedly in anterior outline; however, the difference is attributed to variation in style of dorsoventral compaction rather than to original variation in carapace morphology. Associated trilobites are *Elrathia kingii.*——*1.* Carapace, KUMIP 135134.——*2.* Carapace, KUMIP 135138.

Plate 7

FIGURE

1,2. *Tuzoia guntheri,* n. sp., both from the Marjum Formation, House Range.——*1.* Right valve, partly exfoliated; × 1.0, KUMIP 144390.——*2.* Holotype left valve; × 1.5, KUMIP 153917.

3. *Pahvantia hastata,* n. sp. Incomplete carapace from the Wheeler Formation, House Range; × 1.0, KUMIP 134879.

Plate 8

FIGURE

1,2. *Pahvantia hastata,* n. sp., both from the Wheeler Formation, House Range.——*1.* Incomplete carapace; inferred left anterior part still covered with matrix; × 1.0, KUMIP 134187.——*2.* Holotype carapace, × 2.0, KUMIP 134878.

3. *Tuzoia retifera* Walcott. Left valve with broken posterior margin; from Spence Tongue of the Lead Bell Shale, Wellsville Mountains; × 1.3, KUMIP 153918.

4,5. *Tuzoia guntheri,* n. sp., both from the Marjum Formation, House Range, and both × 1.0. Concentric wrinkles in the central part of each valve are the result of compression.——*4.* Interior view of left valve; anterior end is partly exfoliated; KUMIP 134797.——*5.* Mold of left valve, KUMIP 144982.

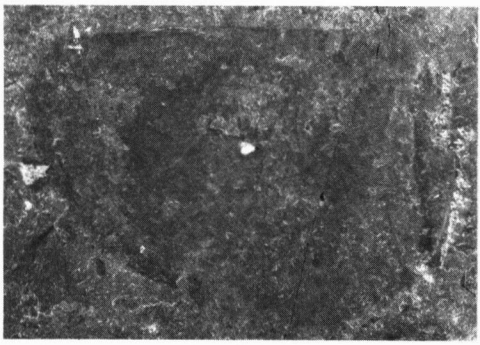
Plate 9

FIGURE

1. *Tuzoia? peterseni,* n. sp. Holotype valve from the Wheeler Formation, House Range; × 3.0, KUMIP 134799.

2. *Tuzoia guntheri,* n. sp. Carapace preserved in parallel aspect; from the Marjum Formation, House Range; height of left valve has been reduced by crumpling of lower part; × 0.8, KUMIP 134798.

3. Genus and species undetermined. Two probable carapaces; small circular objects on surface are sclerites of the agnostoid *Peronopsis interstricta;* × 2.0, KUMIP 134188.



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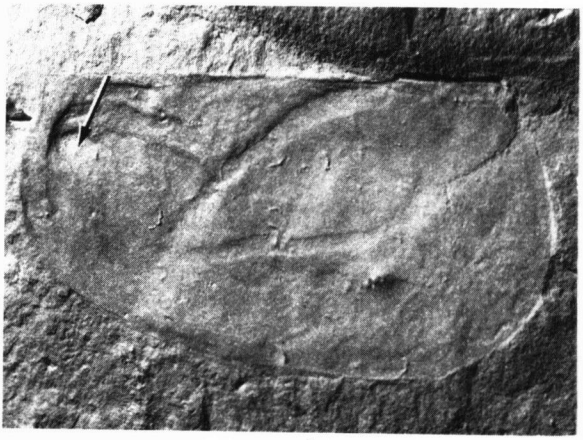

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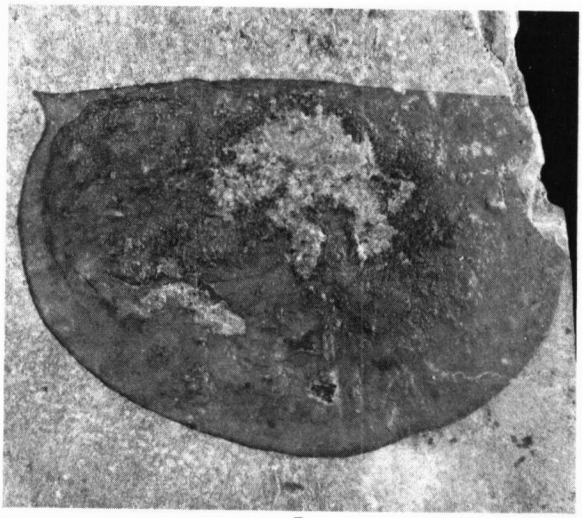

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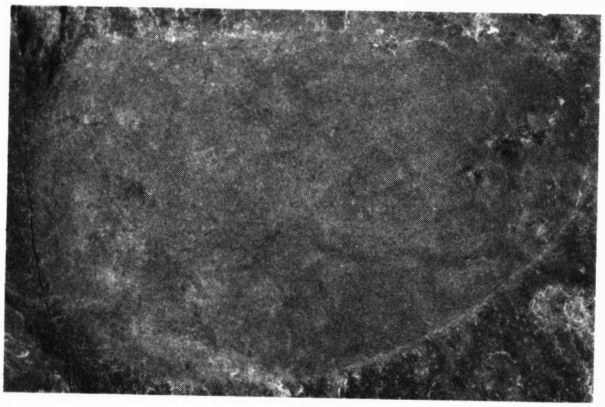

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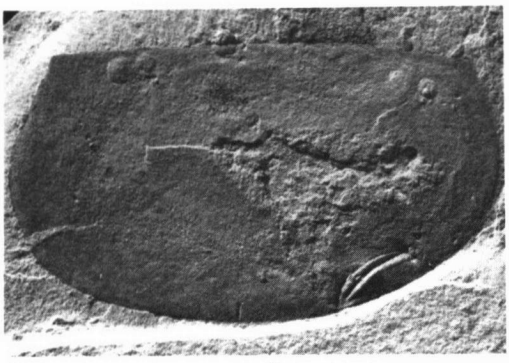

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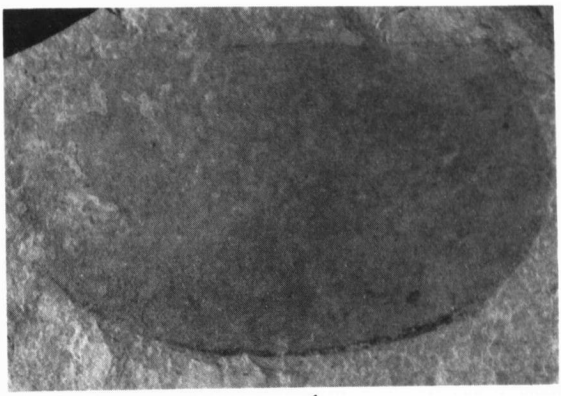

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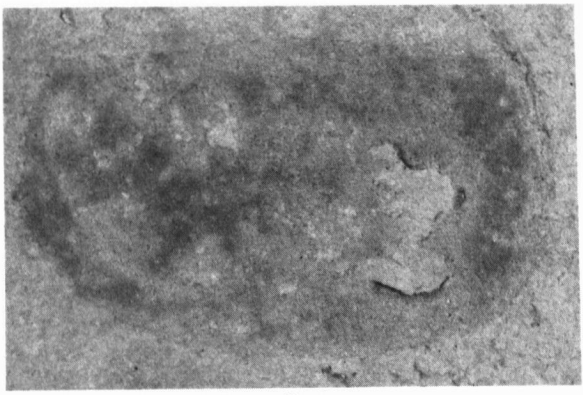

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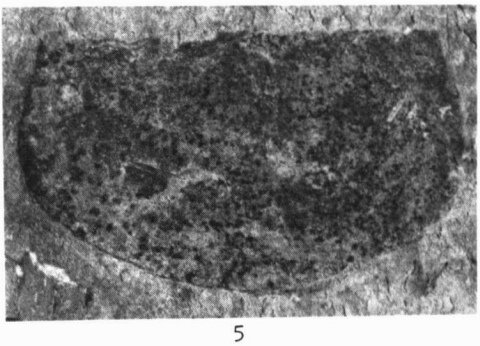

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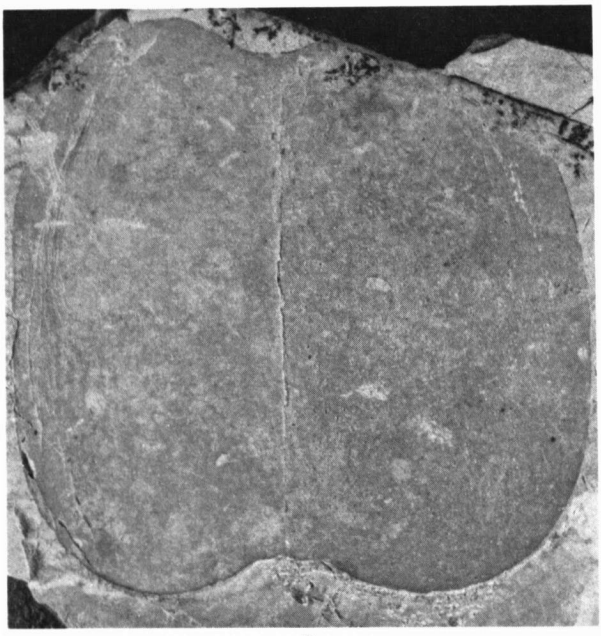

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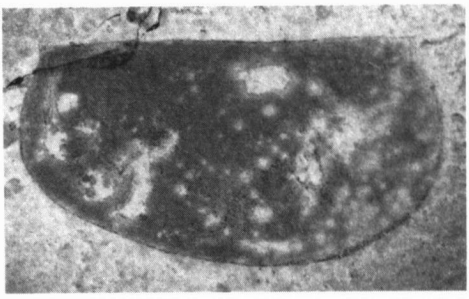

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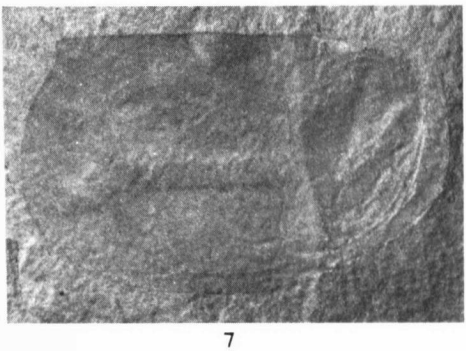

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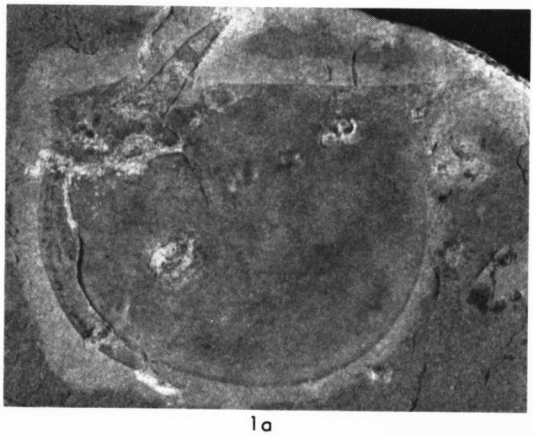

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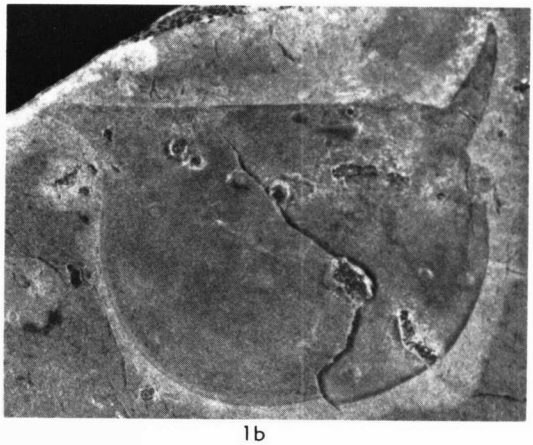

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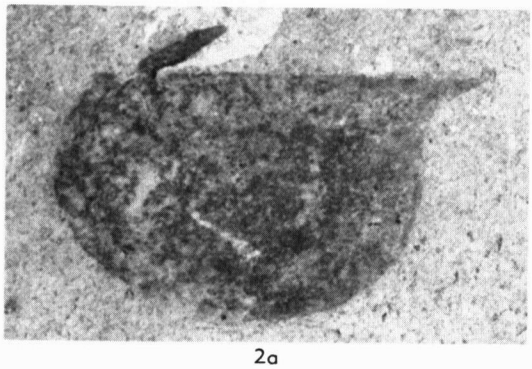

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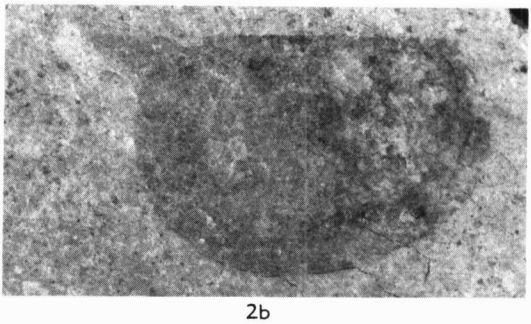

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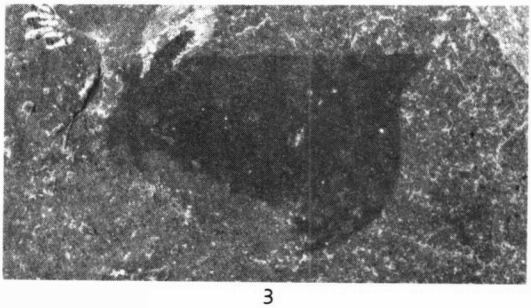

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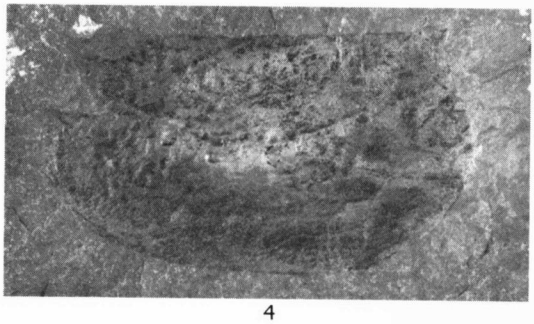

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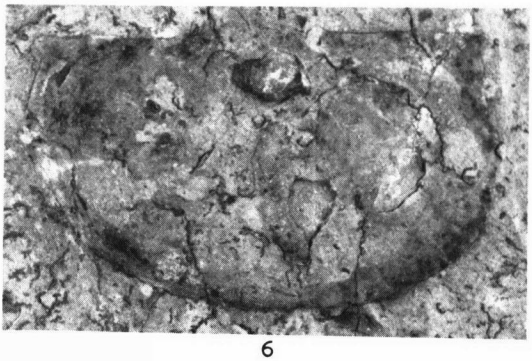

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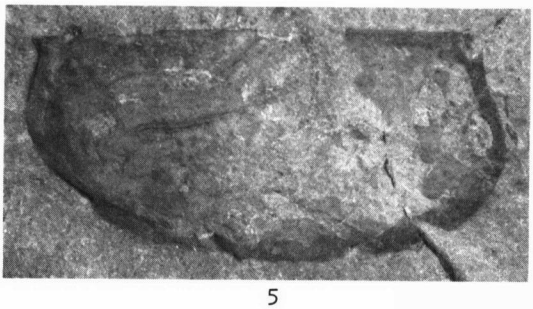

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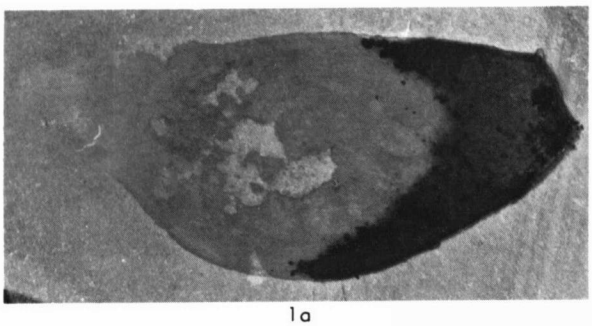

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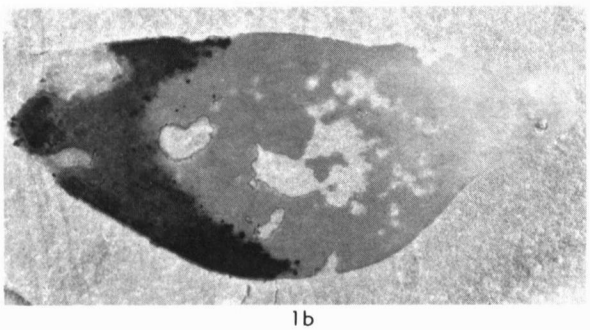

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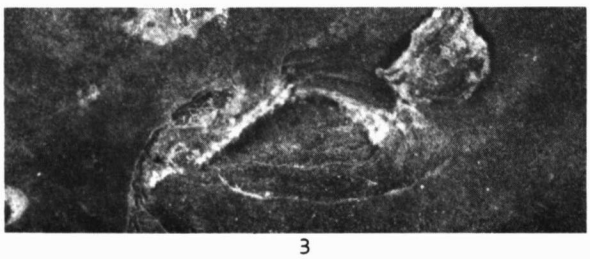

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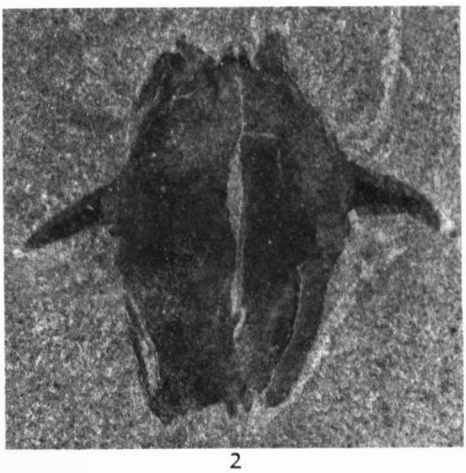

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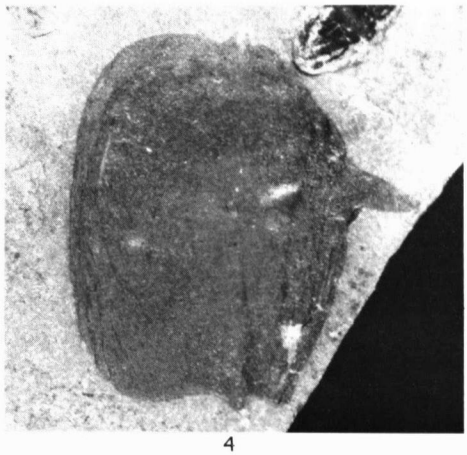

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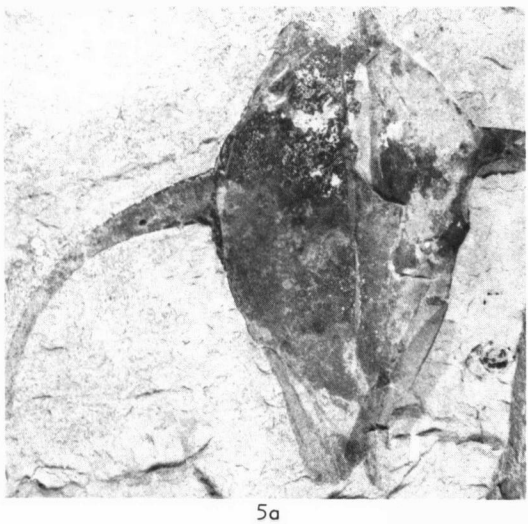

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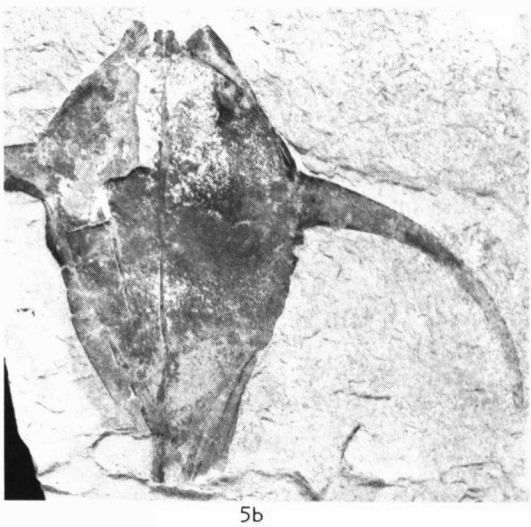

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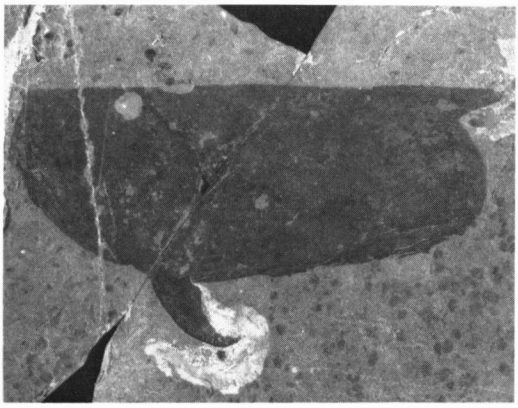

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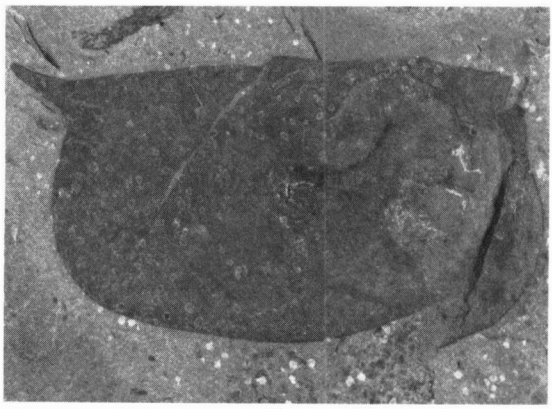

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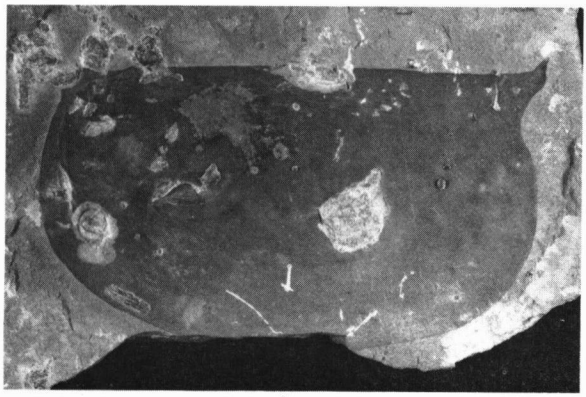

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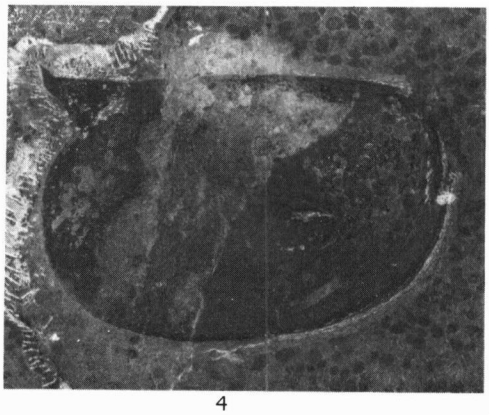

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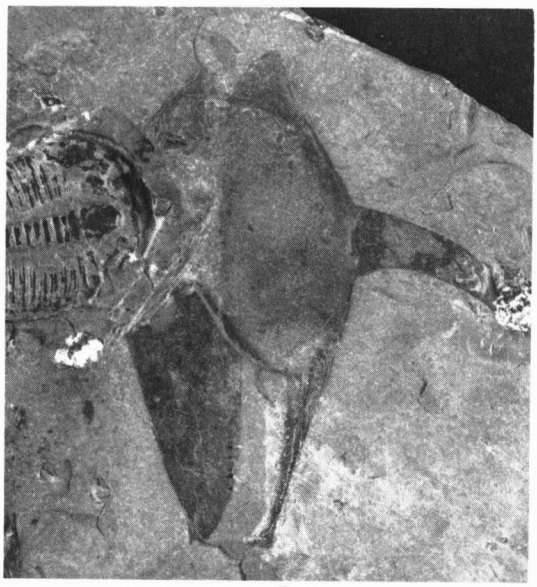

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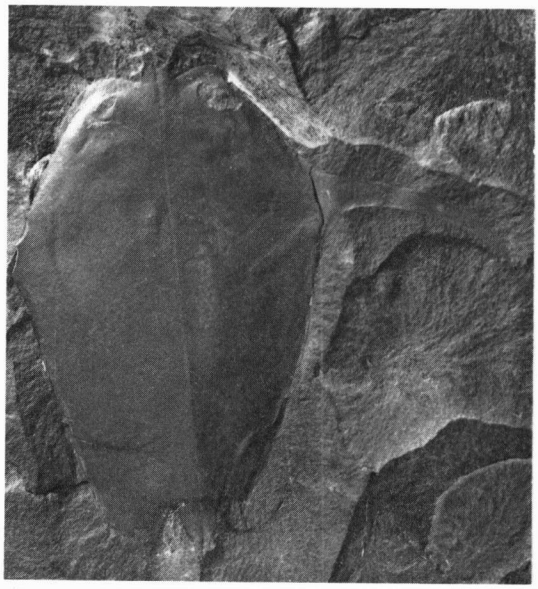

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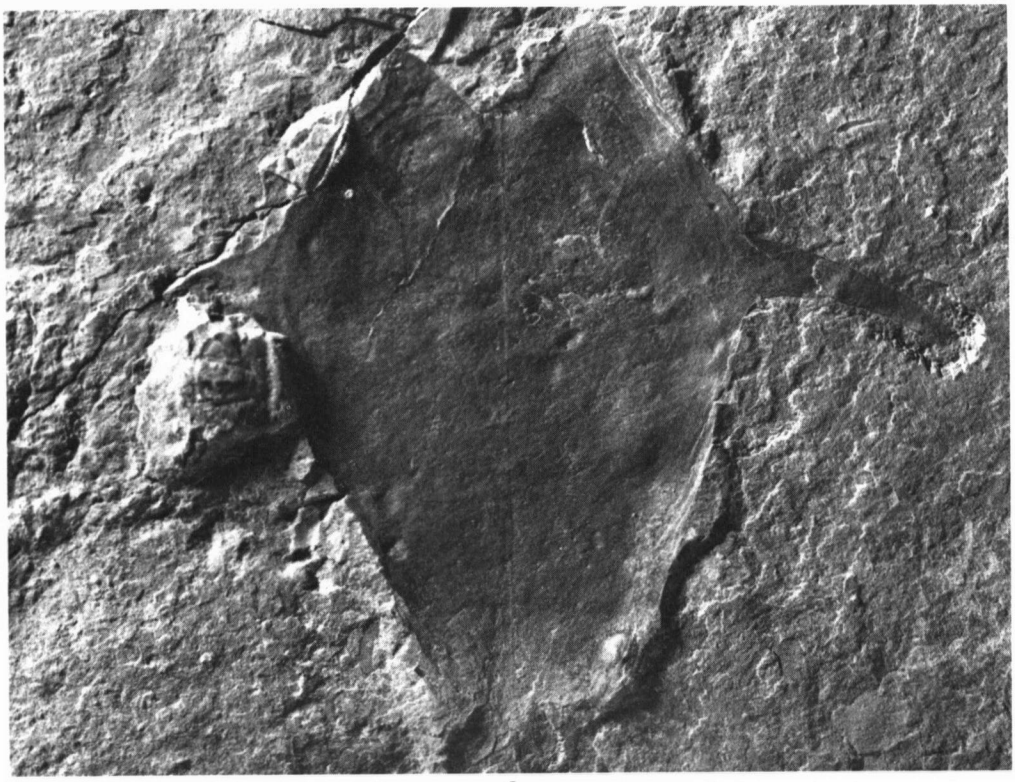

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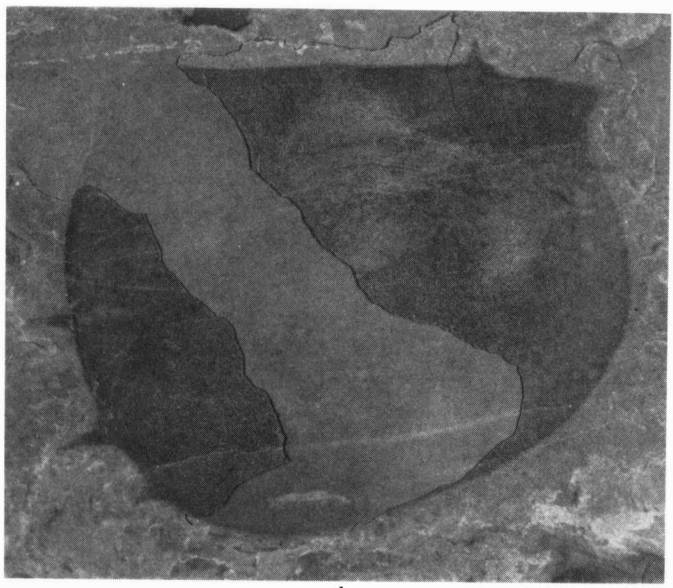

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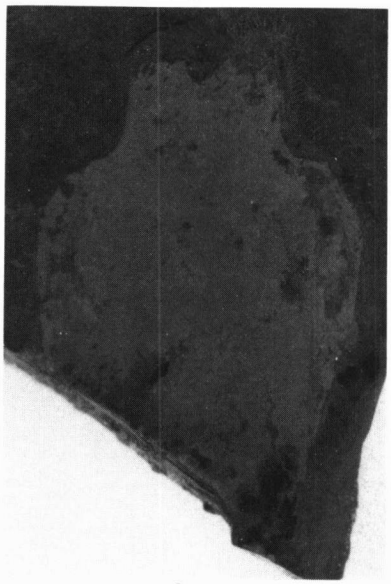

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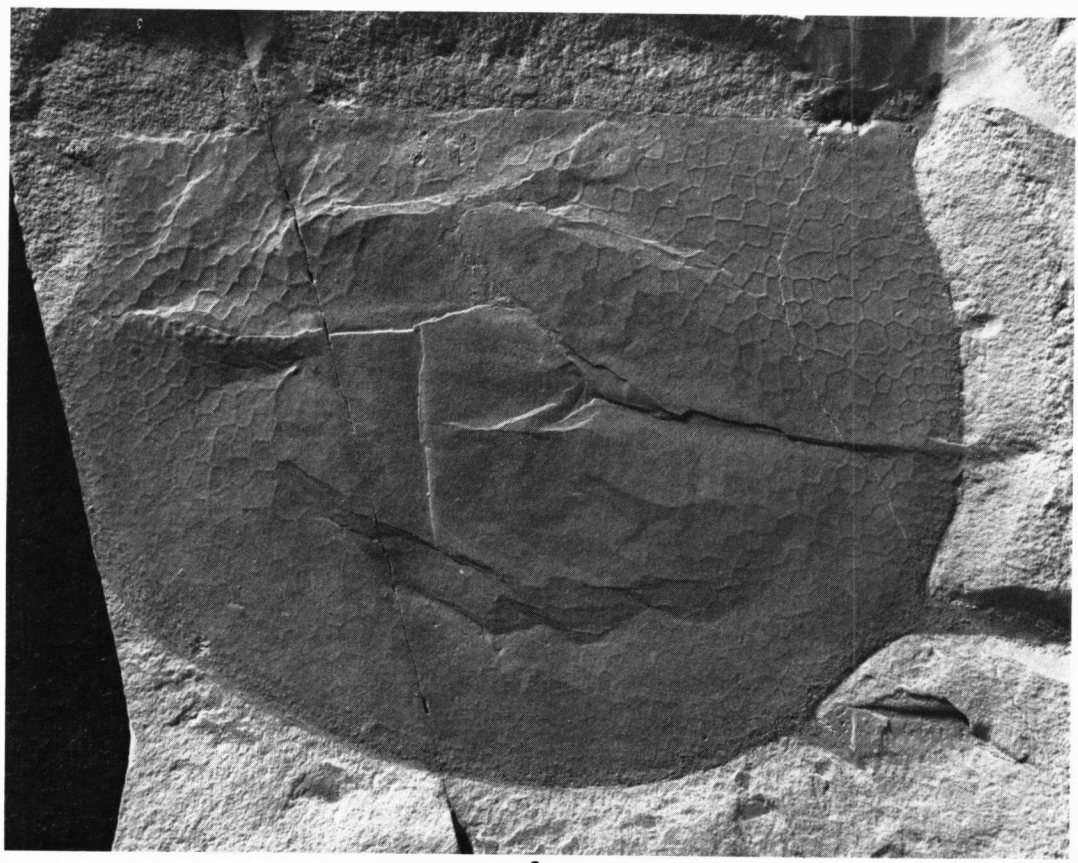

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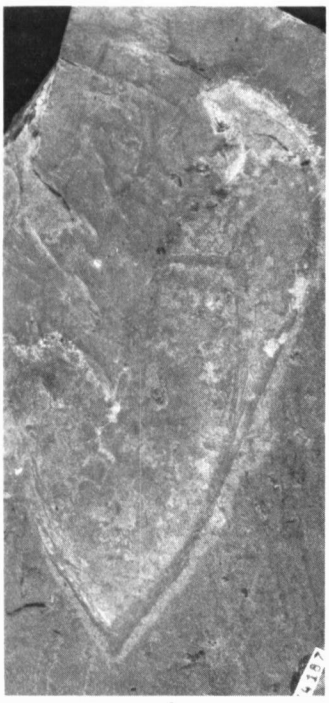

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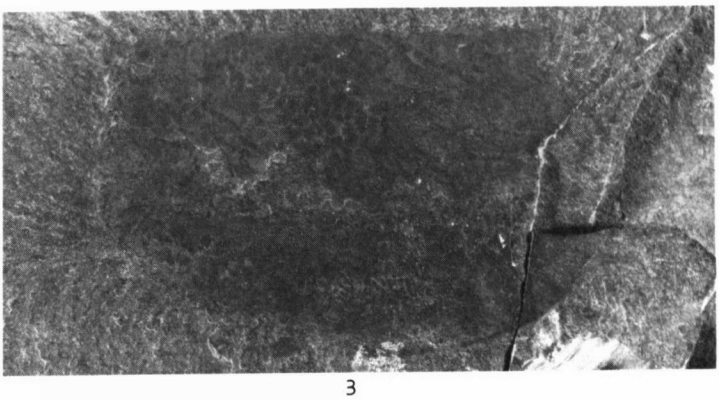

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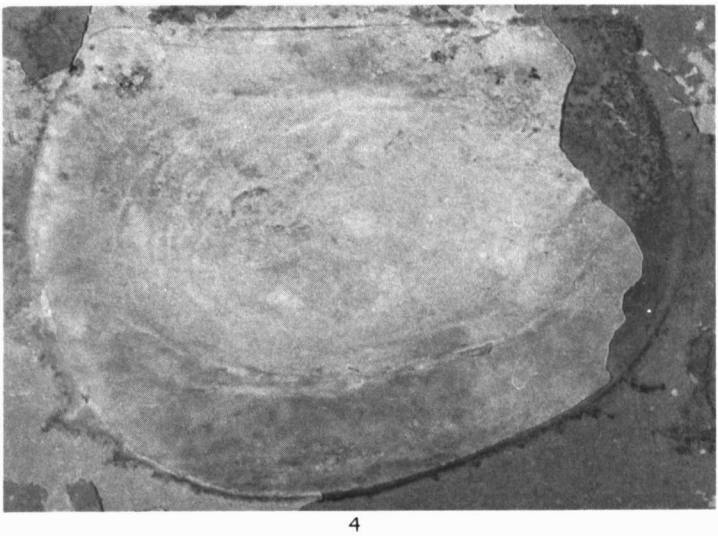

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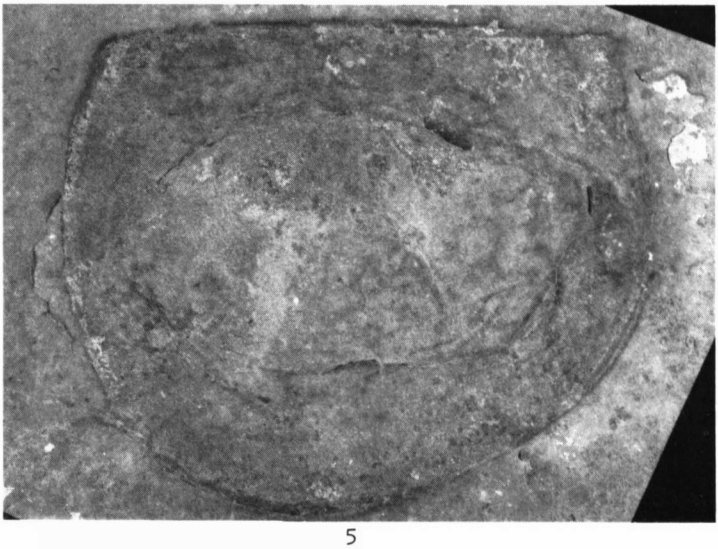

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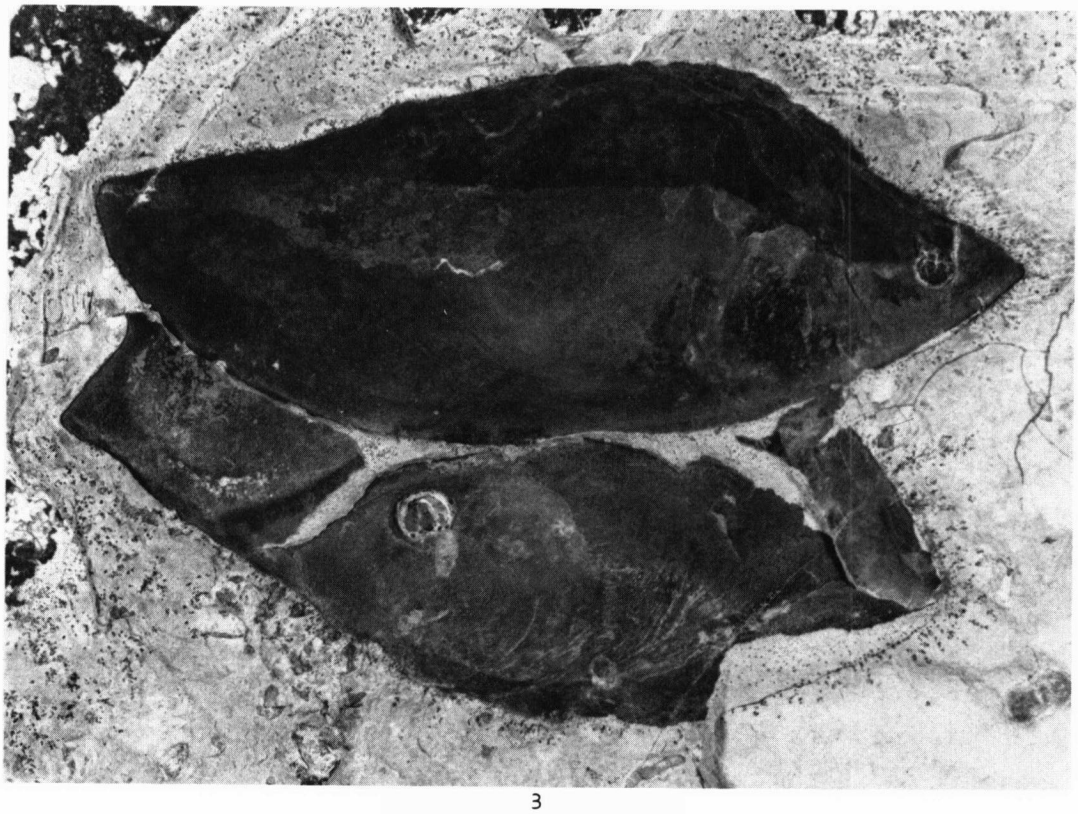

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